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THE SPATIAL METRIC REPRESENTATION
OF BODY PARTS: BEHAVIOURAL AND
NEUROPSYCHOLOGICAL EVIDENCE

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ABSTRACT

The mental representation of the body is being a subject of intensive research from different perspectives starting from the 20th Century. Indeed, the body is a peculiar object for the brain, being at the same time a physical, space-occupying object and the critical mean for perception and action in the world around us. The present doctoral work focussed on the spatial representation of the body; in particular it was investigated whether the body holds a specific metric representation, which is supposed to be useful for action programming and interaction with the environment, as introduced in Chapter 1. To this aim Experimental Part 1 (Chapter 2 and 3) investigated the stable properties of the body metrics, while Experimental Part 2 (Chapter 4) focussed on its plastic and dynamic features.

Chapter 2 discusses the differences between the spatial metric representation of body parts and non bodily three-dimensional objects. In particular, Experiment 1 investigated the possibility that Unilateral Spatial Neglect (USN) may affect to a different extent the spatial analysis of body parts relative to extrapersonal three-dimensional objects. Participants were required to bisect their left forearm and a length-matched cylinder with their right index finger. Both USN patients and neurologically unimpaired participants showed a significantly more accurate estimation of the subjective midpoint of the forearm, relative to the solid object. Besides the main pattern of an advantage in the forearm bisection, a further analysis suggested the possibility of a double dissociation, with two patients exhibiting the opposite advantage in the solid bisection. Experiment 2, asking unimpaired volunteers to perform the same bisection task in three different conditions (Forearm, Fake Forearm, Cylinder), showed a similar kind of spatial analysis for stimuli displaying bodily features, either real or fake, relative to non-corporeal objects. Thus, it can be suggested that the spatial processing of body parts critically depends upon their prototypical visuo-spatial shape and that the spatial metrics of body parts, relatively to non-corporeal objects, is also more resistant to the disruption of spatial processing and representation brought about by USN. *Chapter 3*, starting from recent evidence showing how the body can be used as an intrinsic metric system for the representation of near space,

illustrates how the length of extrapersonal objects can be scaled using the metric representation of body parts, and to what extent a higher-order metric representation of the body relies upon the somatosensory system. Experiment 3 showed, by means of a bisection task, that the spatial encoding of an extracorporeal object (i.e., a cylinder) may be facilitated by the presence of the forearm in that space –i.e. when the forearm was placed inside the cylinder- as if participants can unconsciously rely on its well known metric representation in order to better estimate the length of the cylinder. In Experiment 4 the same task was administered to a group of right-brain damaged patients, with or without somatosensory and proprioceptive deficit, and to a matched control group. The results showed that the spatial metric representation of body parts might be distorted, or even not available, when the somatosensory sensitivity is altered by a cerebral lesion.

Data about the plasticity of the metric representation of body parts are presented in *Chapter 4*. In this last group of experiments, blindfolded participants were required to perform a radial proprioceptive bisection of their forearm before and after a training with a tool, which allowed an extension of the action space in the far space. The results of Experiment 5 supported the working hypothesis that the arm metric representation can be changed by tool-use. In this experiment participants performed a radial bisection of their arm and indicated the subjective midpoint of their arm more distally after the training, suggesting that the perceived length of their own arm was increased. Interestingly, no effect was obtained following a training with a shorter tool (i.e., 20 cm long). Experiment 6 further supported this interpretation by showing, through a proprioceptive control task, that the dynamic lengthening induced in the metric representation of the arm was not due to a mere illusory distal drift of the whole arm. Furthermore, it demonstrated that the spatial metric representations of the dominant and the non-dominant arms share similar plastic features, being both equally prone to be modified by tool use.

In conclusion this doctoral work showed that body size holds a mental representation that is very stable (even more than that of extrapersonal objects), but also characterized by flexible functional plasticity.

CHAPTER 1

GENERAL INTRODUCTION

1.1. The body in the brain: theories and taxonomies

The body represents a special object for the brain, being the interface between oneself and the environment in which people move and act. The mental representation of the body has even been supposed to have an innate origin. Evidence from the observation of newborns suggest that, given their precocious ability to imitate orofacial and head movements, they probably have a basic knowledge of the body structure. This implicit knowledge might be the basis for the subsequent adult body schema (Berlucchi & Aglioti, 1997). Since the end of the nineteenth century philosophers and scientists speculated about the existence of a mental representation of the body. The idea the body and its component parts is represented by the brain was suggested by Munk for the first time (Munk, 1890). In his work he argued that an image of the body is stored in memory and continuously matched with the actual position of the body by the parietal lobe. He hypothesized that this image arises from the early stages of development thanks to the information deriving from first reflexes and locomotion. He further suggested that specific lesions in the brain would have as a consequence a selective damage of the representation of specific body parts, since in his theory each corporeal element has a modular representation stored in a specific area in the somatosensory fronto-parietal cortex. Afterwards, Wernicke postulated a bottom-up theory of the body representation as the results of the merging process of the signals coming from the sensory organs. In his theory he suggested that a stable image of each body part is created by the merging process of the signals coming from vision, touch, muscles, viscera and joints. He called "body consciousness" the overall body image resulting from the integration of all these signals together (Wernicke, 1906). The term "schema", and thus a conception of the body representation as a spatial and topographical representation of the body in space, was first introduced by Bonnier. He referred to a spatially

organized image of body parts in the external space, rather than to a concept of body representation as a mere feeling of existence, or as a mere consciousness of having a body (Bonnier, 1905). In particular he distinguished the notion of "schema" from the notion of "kinaesthesia" (i.e., "*the general sense of existence arising from the sum of the bodily impressions*"). He further specified the spatial feature of the body schema distinguishing between two mechanisms: *the sensorial image*, which allows the perception of a sensory-peripheral information, and *the localization* of the stimulated point, which applies to different sensory modalities providing a common medium. He then described some cases of patients with a disturbance of the body schema; in particular he reported cases of "aschématie" (i.e., the absence of a mental representation of the own body, with the patient having difficulties in localizing the boundaries or the posture of his/her own body parts), cases of "hyper- or hyposchématie" (i.e., the illusory over- or underestimation of the perceived size of the body or of certain body parts) and cases of "paraschématie" (i.e., the illusory mislocation of a body part). Subsequently, the term "schema" has been used by Head and Holmes distinguishing a *superficial schema*, based on the skin surface and used to localize a perceived tactile sensation on the body, from a *proprioceptive and postural schema*. This latter schema (or schemata) was supposed to be the basis of the ability to perceive the position of the body parts into the external space; it would be the result of a continuous updating of the proprioceptive information coming from the voluntary and involuntary movements and thus it would be characterized by an high degree of plasticity. The independence of these two systems would be further supported by the description of a dissociation between the two in a patient who was unable to localize the position of his own hand, while he was still able to localize a tactile stimulus on the skin surface (Head & Holmes, 1911). The notion of "schema" has been then used again by Pick, who actually suggested the existence of several schemata for different bodily elements and for the different sensory modalities. In his theory the body consciousness relies primarily on tactile and kinaesthetic input during the early stages of development, with the role of visual input becoming then more relevant, since in adulthood body representation is supposed to be mainly visual. He described for the first time a case of autotopoagnosia (i.e., the

lack of knowledge about the topography of the body. A typical manifestation is the inability to point to a body part on command), classifying this deficit, as well as the phantom limb phenomenon, as disorders at the level of the body schema. More recent theories, moving from the idea of a purely bottom up constructed body representation, suggested the existence of a genetically predetermined model of the human anatomy. With this respect, Melzack proposed the idea of a neuromatrix, a large neural network on which corporeal awareness relies and that would be able to explain the persistent sensation coming from a missing limb, i.e. the phantom limb phenomenon¹ (Melzack, 1990). He proposed that the persistent activity of this neuromatrix, notwithstanding the loss of the afferent signals from the missing body part, would be erroneously interpreted by the brain as if that body part was still present. Furthermore, he suggested that the spatial distribution and the synaptic links of this network are genetically determined, but even open to the influence of the experience, and thus characterized by an high degree of plasticity. He further supported this latter hypothesis referring to two phenomena:

- The cortical reorganization of the deafferented somatosensory areas occurring after the loss of the afferent signals from a certain body part, with the possibility for these areas to be activated by the stimulation of a different body part. It's the case of phantom sensations induced by the tactile stimulation of the face in patients who had the hand amputated.
- The changing occurring in the shape and size of the phantom limb. In particular it seems that the distal body parts, such as the fingers, persist longer relative to the proximal ones. Furthermore, a telescoping phenomenon is frequently observed, with the phantom hand perceived at its original position immediately after the amputation, but afterwards shortened and even retracted into the stump (Flor, Nikolajsen, & Staehelin Jensen, 2006; Giummarra et al., 2010; Ramachandran & Hirstein, 1998).

¹ The phantom limb is a common phenomenon occurring after the amputation of a limb or its sensory deafferentation. Typically, patients with a phantom sensation report the vivid feeling of still having the missing limb attached to the body and, in the majority of cases, these sensations are painful (Flor et al., 2006).

In line with Melzack, Berlucchi and Aglioti identify the neural substrate of the body representation in three main cortical areas, as indicated by the effects of selective lesions in the network (Berlucchi & Aglioti, 1997). In particular, lesions of the *primary somatosensory cortex* cause tactile and proprioceptive deficits without causing any alteration at the level of body awareness (i.e., anosognosia, somatoparaphrenia, hemisomatoagnosia). On the contrary, the *right posterior parietal lobe* is involved in higher order processes. Lesions of this area can cause both positive (i.e., supernumerary limbs) and negative symptoms (i.e., disownership of a body part). Furthermore, it has been reported that right posterior parietal lesions can suppress phantom limb perception, while excisions of the somatosensory cortex to treat phantom limb pain showed that, with time, both the phantom sensation and the phantom pain return (Melzack, 1990). The *insular cortex* is also supposed to be involved in body awareness, with a specific referral to the emotional aspects, with lesions of this area causing somatic hallucinations (Roper, Lévesque, Sutherland, & Engel, 1993).

Considering the above brief overview of the way the body representation has been conceived in the last 120 years, it appears quite clear how, since its introduction, the term "body schema" has been extensively used in the classical neurology and in the neuropsychological literature, but not always referring to the same concept. Almost all the scientists who approached this issue, in various fields of research (i.e., classical neurology, philosophy, neurophysiology and neuropsychology), have agreed on the plausibility of the existence of a mental body representation, but at the same time, as noticed by de Vignemont, it has generated a huge confusion about the nature and the properties of these notions (de Vignemont, 2010). The natural consequence has been a springing up of slightly different taxonomies focussing on different levels of analysis (i.e., from the mere processes of sensory and multisensory perception, to the study of the interaction between body representation and action, to the study of the body awareness as the developing space of the "self" and its differentiation from the "other"). In her review she suggested that the main criteria used to trace a distinction between different types of body representation have been their availability to consciousness (noetic versus prenoetic), the functional role (action versus perception) and the temporal dynamics

(short-term representations versus long-term representations). With this scheme in mind, three main taxonomies of body representation, suggested in the recent literature, will be now presented: the dyadic model, the triadic model and the online-offline dichotomy.

1.1.1. The dyadic model

One taxonomy supported, with slight differences, by several authors is the *dual or dyadic model* that provides a subdivision into two different representations: the body schema and the body image (Dijkerman & de Haan, 2007; Gallagher, 2005; Paillard, 1999; Rossetti, Rode, & Boisson, 1995). The body schema comprises sensorimotor representations that are useful, if not essential, to guide actions. The body image consists of other kinds of body representations, which are not directly involved in movement execution (i.e., perceptual, conceptual and emotional). The dyadic model is based on the existence of neuropsychological double dissociations, such as between deafferentation and numbsense, or blind touch (Paillard, 1999). Paillard strongly referred his theory to the Ungerleider and Mishkin's dichotomy between the what- and the where-systems (Ungerleider & Mishkin, 1982) and to the dichotomy suggested by Milner and Goodale between vision-for-perception and vision-for-action (Milner & Goodale, 1995). He described the body image as the system to "know where", namely a pictorial representation of the body, mainly based on visual information, dedicated to perceptual identification and recognition of the body parts. On the other hand, the body schema is defined as the system to "know how to get there", namely a sensorimotor map of the body, mainly based on proprioceptive information, dedicated to action execution and thus including information about posture, body parts size and strength (Paillard, 1991, 1999). As mentioned above, he supported his model referring to the existence of two double dissociated neuropsychological deficits: somatosensory-proprioceptive deafferentation and blind touch. In the first case, his patient was not able to point to a body part touched, if not aided by vision, while he was still able to consciously identify that body part even out of sight. He interpreted this deficit as the result of a disruption of the body schema, with an intact body image. In the second case, he reported the case of a patient who, after a complete sensory paralysis of the

right hand following a left parietal lesion, was unable to verbally report any tactile sensation on that hand, while, with her surprise, she was able to point, with the left hand, to the precise tactile stimulated spot on the insensible hand. Thus, this case would be the result of a disruption at the level of the body image, with an intact body schema.

Similarly, Gallagher agreed with a main distinction between a body image, as a system of perceptions, attitudes and beliefs about the body, and a body schema, as an unconscious system of postural and sensorimotor information operating as a guide for action and thus essential to drive the interactions with the environment (Gallagher, 2005). On the contrary, the body image is conceived as a conscious system mainly involved in the sense of self-consciousness and body ownership.

More recently Anema and colleagues reported the case of a double dissociation that would reinforce the theory of a distinction between a "body image for perception" and a "body schema for action" (Anema et al., 2009). Both the patients showed a preserved, but decreased, tactile sensitivity. Patient J.O. showed an impaired body image since she was able to point to a precise tactile spot touched on the contralesional hand, while she failed to localize it by indication on a standard map of the hand. Her deficit cannot be explained by concurrent visual or proprioceptive deficit, as she performed correctly on two control tasks (i.e., (i) to point to neutral visual targets; (ii) to move the arm back to a previous position after it had been moved passively by the experimenter to a different location). Conversely, patient K.E. showed an impaired body schema since he failed in locating a tactile stimulus on his contralesional hand, while his performance was within the normal range when he had to localise the stimulus on a map of the hand.

As suggested by de Vignemont (de Vignemont, 2010), another way to validate the dichotomy body schema/body image is to study the performance of neurologically unimpaired participants in experimental conditions inducing illusory phenomena. To this aim Kammers and colleagues asked blindfolded healthy volunteers to make perceptual and reaching tasks after the induction of an illusory displacement of their forearm (Kammers, van der Ham, & Dijkerman, 2006). The perceptual task consisted in matching the position of the stimulated arm with the unstimulated

one, while the reaching task consisted in making a pointing to the perceived location of the index fingertip of the stimulated arm. The illusion was obtained by vibrating the biceps tendon of right dominant arm, with the result that the brain receives conflicting information about the movement and the position of the stimulated arm. Indeed one tendon gives information that the limb is stretched, while information from the other tendons, the skin and the joints suggests that the position of the arm did not change. The authors hypothesized that the body schema would be less influenced by the illusion. This representation is supposed to be based on proprioceptive information and thus, since there might be more proprioceptive signals informing that the arm is not moving (signals from the triceps tendon, elbow joint and skin VS illusory signal from the biceps tendon), the body-schema-based reaching movement should be less impaired in the illusion condition, relative to the body-image-based perceptual response. Indeed the body image is thought to use stored information about the body; thus, they supposed that in order to resolve the conflict, it might use knowledge about the fact that the stretching of the biceps is a consequence of lowering the forearm. This would lead to the consequence that body-image-based perceptual response are more influenced by the illusion. Their results showed a significantly larger illusory displacement in the perceptual-matching task, than in the pointing-reaching task. Hence, they interpreted this dissociation as a proof of the dissociation between the two body representations. Furthermore, in a second experiment they added a passive matching task in order to avoid any confounding effect due to the active movement of the unstimulated limb by the participant. Interestingly, they found the same significant dissociation between matching, either active or passive, and reaching responses. Additionally, they showed that while both the matching responses were significantly correlated, no significant correlations were found between reaching and matching responses. This results would further support the hypothesis that the two tasks are not based on a single body representation.

1.1.2. The triadic model

Several other authors considered the notion of body image too heterogeneous and suggested a triadic taxonomy in which the body image is split up into two different body representations.

This model keeps the concept of *body schema* as a dynamic sensorimotor map of the body based on afferent and efferent input and mainly involved in providing actual information about the relative position of the body parts in the external space. Then, it describes a *body structural description* and a *body semantics*. The body structural description is conceived as a structural description, mainly based on visual input, of the relation between distinct body parts, such as their boundaries and their positions relative to each other. It is supposed to define the relative position of bodily elements in a perceptual way, which is not influenced by changes in the orientation (Corradi-Dell'Acqua & Rumiati, 2007). The body semantics is described as a linguistic and conceptual representation depicting the functionality of body parts and their categorical belonging (e.g., arm and leg are both limbs; hip and knee are both joints). The dissociation between apraxia, as a disruption of the body schema, autotopagnosia, as a disruption of the body structural description, and body-specific aphasia, as a disruption of the body semantics, is the basis of the triadic model. In particular, Buxbaum and Coslett described the case of a patient (G.L.) who, after a left fronto-parietal trauma, was severely impaired in pointing to body parts on verbal command or imitation and in matching pictures depicting the same body part in different perspectives. On the contrary he was still able to point to animal and object parts, to localize objects placed on his skin surface, as well as to scale his grasp consistently with the size of the object he was asked to reach for (Buxbaum & Coslett, 2001). The authors interpreted his performance as the consequence of a defective body structural description, along with an unimpaired body schema and body semantics. In another study Buxbaum showed the case of a patient (B.G.) who reported difficulties in gesture execution on command and imitation, in matching gestures and in performing mental transformation of body parts. He concluded that his deficit was consistent with a disrupted body schema, namely the dynamic coding of the position of own and other's body parts. The case reported by Coslett and colleagues (Coslett, Saffran, & Schwoebel, 2002) together with the case reported by Suzuki and colleagues (Suzuki, Yamadori, & Fujii, 1997) represent a double dissociation demonstrating the existence of the third type of body representation: the body semantics. The patient studied by Coslett and colleagues exhibited semantic dementia, with a selective sparing of semantic

knowledge about body parts. Additionally, he was able to point to body parts, thus showing a preserved body structural description, and to perform tasks involving the mental transformation of body parts, thus showing a preserved body schema. Conversely, the patient studied by Suzuki and colleagues reported a Broca's aphasia with a selectively impaired comprehension of body parts name, despite preserved comprehension of other words. Regarding the neural bases of the different types of body representation, Buxbaum and Coslett suggested the possibility that the left hemisphere might hold a structural description of both the right and left side of the body, while the body schema would be represented, as in the motor system, in the contralateral hemisphere (Buxbaum & Coslett, 2001). They came to this conclusion observing the differences between the neuropsychological deficits following left-hemisphere lesions (e.g., autotopagnosia, that involve the whole body) or right-hemisphere lesions (e.g., hemisomatagnosia, personal neglect for the contralesional side of the body). More recently Corradi-Dell'Acqua and colleagues used fMRI to identify the neural substrate underlying the body structural description (BSD) (Corradi-Dell'Acqua, Hesse, Rumiati, & Fink, 2008). In each trial participants were presented with two visual stimuli, two human body parts or parts of a building, and they were asked to either identify them or evaluate the distance between them. The authors isolated the neural underpinnings of the BSD analysing the interaction between the factors stimulus and task. In particular they found an activation in the left posterior intraparietal sulcus when participants judged the distance between body parts, thus suggesting that this brain region is involved in the processing of information regarding spatial relationship between the different bodily elements and that its damage could represent the neural substrate of autotopagnosia.

1.1.3. The online-offline dichotomy

Beside the dual and the triadic model, another taxonomy has been recently proposed by Carruthers (Carruthers, 2008). He proposed to override the dichotomy body image-body schema, and provided a model in which he distinguished online from offline representations. Both types of body representation are conceived as being available to consciousness. In

particular, online representations are defined instant by instant and are "*directly plugged into current perception of the body (p.1302)*". They are supposed to be constructed by the actual sensory inputs, thus being synchronically updated and representing the body as it currently is. On the contrary, offline representations are relatively stable in time and describe the body as it usually is. They are constructed from the integration between the online representations, namely the actual sensory inputs, and stored knowledge about the body. Thus, they are supposed to be available to consciousness immediately and also after memory retrieval. He further proposed that phantom limb phenomena in congenital aplasic patients might be explained not only by the existence of an innate offline representation referred to the whole body (see Melzack, 1990), but also with the absence of an online representation of the missing body part. However, as Berlucchi and Aglioti noted, evidence for specific neural correlates of this hypothesized innate body model are still to be determined (Berlucchi & Aglioti, 2010).

1.2. The body in the space

A consistent line of research focussed on the relationship between the body and the space, being the body the means by which people move and act in the surrounding environment. First of all, it's worth noting that the space is supposed to be encoded following a modular organization, including at least three main distinct representations: the personal space (i.e., the space corresponding to the body); the peripersonal space (i.e., the space immediately surrounding the body) and the extrapersonal space (i.e., the farther external space) (Rizzolatti, Fadiga, Fogassi, & Gallese, 1997). In particular, as suggested by several behavioural and neuropsychological evidence, the peripersonal space differs from the far extrapersonal space given that this is the space where vision and touch are optimally integrated (di Pellegrino, Làdavas, & Farnè, 1997; E. Làdavas, di Pellegrino, Farnè, & Zeloni, 1998; E. Làdavas, Farnè, Zeloni, & di Pellegrino, 2000). Furthermore, several evidence showed a tight connection between the peripersonal space and the representation of the body. They are both supposed to undergo a multisensory encoding and are dynamically modified by action. Furthermore, the peripersonal space is thought to be body-part-centred, meaning that the way the external

space is encoded depends on the presence of a body part into that space (Holmes & Spence, 2004). This was first shown in monkeys (Graziano, Yap, & Gross, 1994) and then confirmed in humans (di Pellegrino et al., 1997). Patients exhibiting visuo-tactile crossmodal extinction improved significantly when the ipsilesional visual stimulus was presented far from the hand. Interestingly, when they were asked to cross their arms, so that the left hand laid in the right half of space (and vice versa for the right hand), visual stimuli close to the right ipsilesional hand still induced crossmodal extinction of the tactile stimulus on the left hand. In the crossed condition, the tactile extinguished stimulation occurs in the right unimpaired portion of space, thus showing that extinction is not modulated by the position of the stimuli in the external space. However, as already shown by single-unit recording studies of bimodal neurons in monkey premotor and posterior parietal cortices (Graziano, 1999; Graziano, Hu, & Gross, 1997), it seems that the visuo-tactile peripersonal space is anchored to the hand, changing and moving according to the position of the hand into the external space (see Holmes & Spence, 2004 for a review).

Moreover arm length was found to scale the extent of the peripersonal space in a behavioural study conducted with healthy participants (Longo & Lourenco, 2007). In a previous study (Longo & Lourenco, 2006) the authors found a gradual shift in the attentional bias on a line bisection task going from near to far space. In the subsequent study they asked participants to bisect lines at different distances using a laser pointer. The lines could be within and beyond one's own arm's reach. They estimated the rate at which the shift between near and far space occurs in each subject by computing the slope of the best fitting regression line, calculated by regressing rightward bias on distance. They found a significant negative correlation between the subjective slope and arm's length; thus meaning that people with longer arms showed a lower slope, and hence a more gradual shift in bias with increasing distances. In other words, this means that these subjects have a larger sector of space that they consider as near space, rather than people with shorter arms, and thus they suggested that arm length could be considered an intrinsic metric for the representation of the peripersonal space. Along another line of research, it was further investigated the strict link between body representation and

peripersonal space. Pavani used the crossmodal congruency task to show that the vision of a fake hand, mimicking the position of the real unseen hand, can modulate the magnitude of the interference exerted by visual distractors in a tactile spatial discrimination task (Pavani, Spence, & Driver, 2000). In particular, the interference was stronger when the rubber hands were present and aligned with the hidden real hands, rather than when they were absent. This effect of “visual capture” might depend on the automatic activation of the hand representation induced by the vision of a realistic prosthetic arm; in turn, the space surrounding the fake arm would be represented in the brain as if it was close to the real body part (i.e., visuo-tactile peripersonal space).

The link between the body schema and the peripersonal space is so strong, that Cardinali and colleagues wondered whether they are not two lexical labels actually referring to the same concept (Cardinali, Brozzoli, & Farnè, 2009). They suggest two possible frameworks within which it could be possible to test for their differentiation. One is to study the kinematics of free-hand movements following the use of a tool, being already demonstrated that this manipulation can induce a plastic change in the extent of the peripersonal space. If a modification occurs also at the level of the body representation, then one should expect a change in the kinematics parameters of a free-hand movement performed after tool use, as if the subject was performing the action with a longer arm. The other possibility they suggest is to take time into account. In particular, if the two representations are distinct and based on different neural substrates, then one can predict different latencies for plastic changes to occur in one representation relative to the other and, similarly, that the duration of these effects should be different. In this respect, the present thesis will provide a direct evidence of a plastic change in the metric representation of body parts after tool use, favouring the hypothesis of a distinction between the two spatial representations.

1.3. Body representation, action and tool use

The body schema has historically been conceived as a dynamic map of the body posture which is updated consistently with movement execution (Head & Holmes, 1911). Even other authors,

despite the use of different terms, suggested the existence of body representations which are dynamically modified by action, and thus continuously updated (Carruthers, 2008; Gallagher, 2005). The same process of dynamic adaptation has been demonstrated to occur in the mental representation of peripersonal space (Brozzoli, Pavani, Urquizar, Cardinali, & Farnè, 2009). In this study, they used the crossmodal congruency task to test whether voluntary actions may remap the extent of this multisensory spatial representation. In particular, they asked healthy participants to perform a free-hand movement to grasp an object containing two task-irrelevant visual distractors (i.e., two flashing LEDs placed at the two vertical endpoints of the object). In the meantime (i.e., at the movement onset in one condition, and during the early phase of movement in a separate condition) they had to discriminate the vertical position of a tactile stimulus delivered at the index finger (i.e., up) or at the thumb (i.e., down). Comparing the two action condition with a static condition (i.e., participant performed only the perceptual task) they found that reach-to-grasp movements increased the crossmodal interference effect of the visual distractors on the tactile discrimination task; furthermore this modulation was specific for the hand used to perform the movement. They thus suggested that, from the very beginning of action programming and during the entire length of the movement, the relationships between vision and touch are reweighted. Indeed this is demonstrated by the fact that visual distractors, located on the target of the action, interfere stronger with the tactile stimuli on the hand involved in the movement execution, relative to a static condition in which no action is required. Along a similar line of research, other studies had already demonstrated a remapping of the extent of the peripersonal space by means of paradigms in which participants were trained to use a functional tool. Iriki and colleagues first showed that the response of single neurons in the intraparietal sulcus of the monkey brain can be modulated by tool-use (Iriki, Tanaka, & Iwamura, 1996). These neurons are known to show a bimodal response, being activated by a visual stimulus near the hand or a tactile stimulus on the hand (distal-type neurons), and by a visual stimulus in the space reachable by the hand or a tactile stimulus on the arm and the face (proximal-type neurons). The authors showed that, after a training of 15 minutes with a rake used to retrieve some food in the far space (i.e., unreachable without using the tool), the visual

receptive field of the distal-type cells expanded to include the space occupied by the rake, while the visual receptive field of the proximal-type cells expanded to include the whole reachable space allowed by the tool use. Additionally, the same research group showed in a PET study the activation of the intraparietal and premotor cortices after skilful use of a tool, relative to random use (Obayashi et al., 2001). Furthermore they observed that with an extensive training, lasting at least 3-4 weeks, many neurons acquire bimodal receptive fields, along with a local increase in the level of neurotrophic factors, signalling a specific gene induction (Ishibashi et al., 2002a, 2002b).

In parallel, other research groups studied the same phenomenon in humans. Here the relationship between body representation, action and tool-use becomes even more interesting and important from a practical point of view if we think that this knowledge could add further insight to the use of special tools such as functional prostheses. Within a more philosophical framework, De Preester and Tsakiris suggested to trace a distinction between "body extension", which would occur in the case of tool-use, and "body incorporation", which would occur in the case of successful prosthesis use and acceptance. Only in the latter case, indeed, a change in the sense of body ownership is supposed to be involved, with, ideally, a relation of completion between the prosthesis and the holder (De Preester & Tsakiris, 2009). They claim for a body model which would define some constraints to body incorporation: non corporeal objects, such as prosthetic limbs, have to fit with this predetermined normative model regulating their incorporation on the basis of their resemblance with real body parts. The likeness would be evaluated on the basis of postural, visual and anatomical clues. In contrast, they suggest that extensions of the body representation by means of functional tools, would involve bottom-up modifications in motor and perceptual capacities, without any change occurring in the feeling of body ownership. Thus, they conclude that in the case of extension the body model is not a constraint, being the relation between body and tools a more external process, relative to the incorporation of an artificial body part replacing a missed or absent limb.

Besides this philosophical account, several other research groups investigated the relationship between body representation, action and tool-use from a more neuroscientific point of view. For

example, Maravita and colleagues showed that the active use of a tool can change the pattern of crossmodal interference exerted by visual distractors on tactile stimuli (Maravita, Spence, Kennet, & Driver, 2002). First they started from the fact that this effect has been repeatedly reported to be stronger for visual distractors located at the same side of space as the stimulated hand; in other words, in a tactile localization task an upper/lower right visual stimulus interferes stronger respectively with a lower/upper tactile stimulus delivered on the right hand, than on the left hand (C. Spence, Pavani, Maravita, & Holmes, 2008). Then, they showed that this modulation reverses when participants actively held two golf clubs and crossed their tips across the midline; in this way each golf-club-hand was virtually connected to the opposite visual hemifield and thus the visual distractors located in the contralateral side of space, relative to the tactually stimulated hand, became more effective in inducing a crossmodal interference effect. Importantly they observed, in a control experiment, that the reversal did not occur if participants passively held the tools, which were crossed only at the end of each block, rather than every 4 trials. They concluded that a new functional link between vision and touch was created at the tip of the tool following tool-use, thus inducing a stronger interference effect as if the visual distractors were presented close to the skin. In other words they interpreted these results as if the active use of a tool had induced its inclusion into the body schema. More recently Kao and Goodale demonstrated an enhanced visual detection for stimuli presented close to the participants' real hand, than for stimuli presented on a fake hand or on a small garden rake. However, after a brief training with one of the two non-corporeal objects, participants showed faster responses to visual stimuli presented on the object they had been trained with, while their performance did not change for stimuli presented on the other object. The authors interpreted these results as the consequence of the incorporation within the body schema of the inanimate objects previously used with a functional purpose during the training (Kao & Goodale, 2009).

Several other studies in the neuropsychological literature showed the same modulation of visuo-tactile interactions after tool-use. For example, Farnè and Làdavas demonstrated that, after a training with a rake used to retrieve objects in the far space, patients with crossmodal visuo-

tactile extinction exhibited a stronger deficit when the visual concurrent ipsilesional stimuli were presented in the far space, relative to the extinction rate exhibited for the same stimuli before the tool-use (Farnè & Làdavas, 2000). In a closely related single case study, it was described a patient who reported an higher visuo-tactile extinction rate when he actively held the tip of a stick close to the visual stimuli in the far space, relative to a condition in which the stick was absent or present but physically disconnected from the patient's hand (Maravita, Husain, Clarke, & Driver, 2001). This latter result demonstrates that in order to obtain a tool-dependent change in the extent of the peripersonal space, it is necessary to use an effective, functional tool. As shown by Farnè and colleagues, indeed, if the functional part of a tool is positioned midway, and not at the tool tip, visuo-tactile effects occur at the location where the effective part is positioned, instead of at the physical end of the tool (Farnè, Iriki, & Làdavas, 2005). The studies presented above have shown that the extension of the peripersonal space following tool use lasts for brief time interval, with return to the baseline extent a few minutes after the end of the training (Farnè & Làdavas, 2000). However, sometimes tools are used in everyday life for prolonged periods of time, such as the case of blind people using a cane. Serino and colleagues demonstrated the existence of a stable expansion of the peripersonal space in blind cane users; indeed they were faster in responding to tactile stimuli when a concurrent, task-irrelevant auditory stimulus was presented at the tip of the cane, rather than close to the hand (Serino, Bassolino, Farnè, & Làdavas, 2007). Conversely, sighted participants, who never experienced the use of such a cane, were faster when sounds were presented close to the tactually stimulated hand, demonstrating the existence of a peri-hand space in which audition and touch are integrated. It was additionally demonstrated that, after a 10 minutes training with a blind cane, healthy participants' audio-tactile peripersonal space can be extended to include the tool, with reaction times to tactile stimuli associated with a near sound being equal to those associated with a far sound.

The working hypothesis, that almost all these studies have in common, is that the expansion of the peripersonal space following tool-use can be interpreted as the consequence of a corresponding dynamic expansion of the body representation to include the tool as a functional

extension of a limb. In other words, they based their interpretation on an indirect measure, drawing a putative parallel between changes in the representation of the peripersonal space with a consistent change in the representation of the body.

Cardinali and colleagues tried to overcome this theoretical limitation by a motion-capture study in which the kinematics of a free-hand movement is measured before and after the use of a functional tool (Cardinali, Frassinetti et al., 2009). They reported an alteration of the kinematics of a free-hand grasping performed after a brief training with a 40 cm-long mechanical grabber, physically extending the reachable space. The modification in the parameters they measured, and in particular a slowing down of the peak velocity of free hand reaching movements, were interpreted as being consistent with an alteration of the represented arm, as if the arm was longer than it was before the training. Interestingly, such a tool-use after-effect was found to generalise to untrained pointing movements. Additionally, after the training, participants localized light touches on the elbow and the middle fingertip as if they were farther apart, thus indicating an increase in the represented arm length. Further details about this experiment will be provided in Chapter 4 where new data about the tool-use-dependant changes in the metric representation of body parts will be presented.

1.4. Aim of the doctoral work

The complexity of the research about body representation is well illustrated by the evidence presented so far, with the obvious consequence that different points of observation can be adopted. Some authors tried to define a taxonomy in order to achieve a shared definition and use of the different terms and concepts referred to the way in which the brain represents the body. Besides the efforts to clarify these theoretical aspects, different methodologies have been used, focussing on different sides of the issue. Thus, a number of works investigated the mere sensory and motor processes connected to body representation, discovering for example which brain areas are involved in the visual recognition of body parts (Downing, Jiang, Shuman, & Kanwisher, 2001); other research work focussed on the study of the relationship between body schema, space and action programming (Brozzoli et al., 2009) and on the dynamic properties of

body representation (see for a review (Cardinali, Frassinetti et al., 2009; Farnè, Serino, & Làdavas, 2007). A different line of research involves the sense of body ownership (Tsakiris, Costantini, & Haggard, 2008; Tsakiris & Haggard, 2005; Tsakiris, Hesse, Boy, Haggard, & Fink, 2006; Tsakiris, Longo, & Haggard, 2010; Tsakiris, Prabhu, & Haggard, 2006) and the sense of the self, basically defined as a process that makes possible to distinguish oneself from the others (Devue & Brédart, 2010; Gillihan & Farah, 2005; Sugiura et al., 2006).

The present doctoral work is focussed on the spatial representation of the body; in particular, it is aimed at verifying the existence of a metric representation of body parts (Chapter 2) and at clarifying its properties (Chapters 3 and 4).

1.5. Summary of the work

1.5.1. Experimental part 1

In the first part of this thesis the spatial metric representation of the body and its stable properties were investigated in healthy participants and in neurological patients.

Chapter 2 provides evidence for the existence of a metric representation of body parts, showing that their spatial analysis is facilitated relative to non corporeal objects. Experiment 1 investigated the possibility that Unilateral Spatial Neglect (USN) may affect to a different extent the spatial analysis of body parts relative to extrapersonal three-dimensional objects. Furthermore, while several studies investigated bodily aspects of the neglect syndrome, there is still lack of information about any possible impairment of the spatial metric of body parts in USN. Patients, selected on the basis of the presence of USN as assessed by a complete neuropsychological battery, were required to bisect their left forearm and a length-matched cylinder holding the same position within the peripersonal space. A matched control group of healthy participants performed the same task. The bisection task was chosen because it involves a spatial analysis of the target both in neurological unimpaired participants (Jewell & McCourt, 2000) and in USN patients, who typically misplaced rightward the subjective midpoint of the target (e.g., a line, a string of letters or number, etc. etc.) (Bisiach, Bulgarelli, Sterzi, & Vallar, 1983; Halligan & Marshall, 1988; Heilman & Valenstein, 1979). The most interesting

result was that both the groups showed a significant smaller error in the forearm bisection compared to the cylinder bisection, indicating that in both the groups the estimation of the subjective midpoint of the forearm was significantly more accurate than that of the solid. Furthermore, using the Revised Standardized Difference Test (Crawford & Garthwaite, 2005), the difference between solid and forearm bisection in each patient was compared to the same difference in the neurologically unimpaired participants. Besides the main pattern of an advantage in the forearm bisection, this latter analysis suggested the possibility of a double dissociation, with two patients exhibiting an opposite advantage in the solid bisection. Even if Chapter 2 provides, along with further details, a mapping of the lesions, no definitive conclusions concerning the anatomo-clinical correlation of this double dissociation can be drawn due to the small number of relevant patients.

Experiment 2 specifies the main result obtained in Experiment 1, namely that discrete and independent mechanisms may control the spatial processing of the length of corporeal relative to extracorporeal objects, with the former having a more stable metric representation. In particular, in this second study, neurologically unimpaired volunteers performed the same bisection task on three different target conditions (real forearm, fake forearm and cylinder) using alternatively the right or the left index finger. The working hypothesis was to find a superiority for the spatial analysis of body parts as compared to extra-corporeal objects further clarifying whether any possible difference in the spatial coding of real and fake body parts could be mainly due to a richer sensory input from the body, or to the prototypical shape of bodily segments. Overall participants showed a similar amount and direction of error in the bisection of a real or a fake forearm relative to the same task performed on a cylinder, thus suggesting a similar kind of spatial analysis for bodily elements, either real or fake, relative to non-corporeal objects. Additionally, the performance in the forearm and fake-forearm conditions appeared to be independent from the hand used to perform the task. This result suggests the existence of a quite stable metric representation of body parts that would act as a reference point, making the performance more stable and not open to the influence of such external variables. Given the results of the first experiment, the body part metrics would be also more resistant to the

disruption of spatial processing and representation brought about by USN, relatively to non-corporeal objects. Moreover, it seems that the advantage emerged for the body depends upon the activation of a visuo-spatial representation of the prototypical shape of the body and that coding the length of body parts and of extrapersonal objects are dissociable functions.

Chapter 3 reviews recent evidence showing how the body can be used as an intrinsic metric system for the representation of near space suggesting, in particular, that the distance of objects may be scaled as a proportion of one's arm length (Longo & Lourenco, 2007). In particular, Experiment 3 illustrates how the length of extrapersonal objects can be implicitly scaled by using the metric representation of body parts, while Experiment 4 shows how important is the availability of a well-working somatosensory-proprioceptive system to maintain and use an efficient higher-order metric body representation. In Experiment 3, a bisection task of a cylinder in two different conditions (i.e., "Empty Cylinder" and "Cylinder plus Forearm", namely with or without the left forearm placed into the three-dimensional object) was administered to a group of neurologically unimpaired participants. The main hypothesis was that if the metric representation of a body part (i.e., the forearm and the hand) can be used to scale the length of a non corporeal object, then participants should show a better performance in the former condition, relative to the latter one. In agreement with the experimental hypothesis, the results showed that the spatial encoding of an extracorporeal object (i.e., the cylinder) may be facilitated and may become more efficient thanks to the presence of the forearm in that space. This finding suggests that, when the forearm was placed inside the cylinder, participants can unconsciously rely on a well known metric representation of the forearm which actually corresponds to the length of the cylinder. These results are in line with the study of Longo and Lourenco that demonstrates how body parts length, being used as an intrinsic metric parameter, can determine the extension of the peripersonal space (Longo & Lourenco, 2007), but also further specify this issue by suggesting that the presence of a body part actively scales the metric judgement relative to extrapersonal objects in its surrounding space.

In Experiment 4 the same bisection task was administered to a control group and to a group of right-brain damaged patients with or without tactile and/or proprioceptive defects (respectively SP+ and SP-). Similarly to Experiment 3, healthy participants and SP- patients showed a lower deviation score in the "Cylinder plus Forearm" condition. Conversely, in this condition SP+ patients exhibited an higher errors, indicating that the spatial metric representation of body parts might be distorted, or even not usable, when the somatosensory sensitivity is altered by a cerebral lesion. Additionally, the difference between the two bisection conditions in each patient was compared with the same difference in the control group using the Revised Standardized Difference Test (Crawford & Garthwaite, 2005). No patients in the SP- group showed a difference relative to the control group, confirming that their performance can be considered in line with healthy participants' one; on the contrary all the patients within the SP+ group showed a significant difference relative to the healthy participants. Recent evidence showed the strict relation between somatosensory input and higher-order body representation, being for example the perceived size of objects held between the fingertips distorted when cutaneous input were blocked by anaesthesia (Berryman, Yau, & Hsiao, 2006), and being the perceived size of the thumb altered after a complete anaesthesia (Gandevia & Phegan, 1999). Thus, a possible interpretation of the present results might be that in the lack of somatosensory information regarding the forearm, its metric representation is less defined, mimicking the case of somatosensory deafferentation. In conclusion, Experiment 3 and 4 suggest that the spatial metric representation of body parts may implicitly influence the spatial coding of extrapersonal objects that share a common space with the body; furthermore it seems that a similar effect is based on the availability of efficient tactile and proprioceptive information.

1.5.2. Experimental part 2

The second part of this thesis is focussed on the plastic properties of the spatial metric representation of body parts. In particular, *Chapter 4* reviews the literature about the interaction between mental body representation and the use of functional tools, especially referring to the their hypothesized inclusion into the boundaries of the so-called body schema.

In this last group of experiments participants were required to make a radial proprioceptive bisection of their arm before and after a training with a 60 cm-long tool, which extended their reachable space. In Experiment 5 they sat blindfolded on a chair with their right forearm placed on a support on the right side. A transparent screen was placed above the arm in order to avoid any tactile feedback during the body bisection task, which could have biased the performance by providing a tactile anchor for the bisection. Participants were instructed to set the radial midpoint of their forearm (considered from the elbow to the tip of the middle finger) with their left index finger, following a vocal cue given by the experimenter. A paper rule was placed on the top of the plastic screen, with one extreme (0cm mark) placed exactly above the tip of the middle finger. After each trial the experimenter noted down the point (p) indicated by the participant. Afterwards a percentage score was calculated by means of the following formula: $[(p/\text{length of the arm}) * 100]$, with a value higher than 50% indicating a proximal deviation of the subjective midpoint (namely, towards the elbow) and a value lower than 50% indicating a distal deviation (namely, towards the hand). The results showed that after the training participants tend to perceive the midpoint of their arm more distally. This finding seems to support the working hypothesis of a modification in the metric representation of the arm by tool-use. Thus, it seems that after the use of the tool participants perceived their arm as longer than in normal conditions. Furthermore, a control study replicating exactly the same experimental setting and procedure, except for the tool length (i.e., 20 cm instead of 60 cm; see paragraph 4.3.2. for details), seems to exclude that the observed illusion of having a longer arm could be simply due to the fact of having performed goal-directed actions in the space in front. Indeed, in this study no differences were shown between the pre and post training arm bisection task. This finding additionally shows that the length of the tool, and thus the degree of extension of the reachable far space, seems to be a crucial characteristic in order to generate the illusion of having a longer arm, and hence in order to determine a dynamic change into the spatial metric representation of body parts.

Experiment 6 further specifies the result obtained in Experiment 5. First of all, a proprioceptive matching task was included in order to exclude that an illusory drift of the perceived position of

the whole arm away from the body, according to the direction of the actions performed during the training, was responsible for the observed distal shift in the bisection task. Thus, blindfolded participants were asked, after each block of bisections, to match the position of the trained arm with the untrained one (see paragraph 4.4.1.2. for details). Secondly, in order to investigate whether the representation of the dominant arm was more prone to be modified by tool use, being more often used to manipulate tools relative to the non-dominant one, participants performed the training alternatively with the dominant and the non-dominant hand.

Relative to the first question, overall participants made a slight error in the position matching task, indicating a slight proximal misperception of their trained arm relative to its actual position; interestingly this trend did not show any difference between the pre and post-training sessions, thus meaning that the tool use did not cause any illusory proprioceptive misplacement of the whole arm and hence confirming the main finding of Experiment 5. Concerning the second question, a repeated measures ANOVA showed that both the spatial metric representations of the dominant and the non-dominant arm are equally prone to be dynamically modified by tool use.

The results of Experiment 5 and 6 are discussed in light of the recent findings about plastic changes in the peripersonal space representation and in the body schema after tool-use (Bonifazi, Farnè, Rinaldesi, & Làdavas, 2007; Cardinali, Frassinetti et al., 2009; Farnè et al., 2005; Farnè et al., 2007; Maravita, Spence et al., 2002). In particular, referring to the recent question regarding the possible overlapping between these two concepts (Cardinali, Brozzoli et al., 2009), the findings reported here seem to favour overall the hypothesis of independence of the two mental representations.

CHAPTER 2

THE SPATIAL METRIC REPRESENTATION OF BODY PARTS AND NON-BODILY OBJECTS

2.1. Mental representation of the body: the personal space

The body allows us to move in the external world and receive sensory information not only from the surrounding environment (i.e., exteroception), but also from the inside of the body itself (i.e., interoception). Thus, an efficient mental representation of the body is critical for our survival and it's not surprising the existence of "body dedicated" brain areas. One of these, the lateral occipito-temporal Extrastriate Body Area (EBA), is selectively activated by the vision of real and stylized images of human body parts, belonging to one's own or to someone else (Downing et al., 2001). Furthermore, it was demonstrated the existence of another region, functionally distinct from EBA, in the occipito-temporal cortex responding to the haptic presentation of body parts (HBR, Haptic Body Region) (Kitada, Johnsrude, Kochiyama, & Lederman, 2009). The existence of such brain regions suggests that a variety of body-related information, coming from the visual and from somatosensory and proprioceptive channels, gives rise to a complex mental representation of the body. In order to efficiently act in the surrounding space we need not only a representation of the position of the body in space, but also information about the size and length of body parts as well as their relative spatial relations. Part of this information might be stored in memory as a stable representation (i.e., the anatomical structure of the body and the spatial relations between contiguous body parts, such as the fact that "the hand is connected to the forearm by the wrist"), whereas other information needs to be constantly updated (i.e., the actual position of each body part during movement execution). It can be hypothesized that the first type of information acts like a template of the body, a sort of body model used, for example, to identify the source of a somatosensory stimulation. The second type of input would be essential for the programming

and monitoring of actions. All these information interact in the healthy brain so that any movement in daily life can be performed smoothly and precisely. A critical feature that the brain has to take into account for movement execution is the metric of the body. In particular it is reasonable to suppose that the brain holds a stored knowledge about body parts size and length. Any short-term, online updated information would be efficiently merged with such a stored and stable knowledge about the body in order to allow quick and efficient movement execution (de Vignemont, 2010). One important question is which kind of information the brain uses to generate this body representation. In this respect, there is much evidence about a strict interaction between visual and somatosensory information related to the body (see for review (Macaluso & Maravita, 2010). For example, crossmodal congruency effects in normal subjects seem to support the idea that the peripersonal visual space around the body may be represented along with the somatosensory one, being the interference effect of visual distractors on tactile stimuli particularly stronger for visual distractors near the hands, as compared to those far from the body (Maravita, Spence, & Driver, 2003). Studies in crossmodal visuo-tactile extinction patients further suggest the existence of an integrated visuo-tactile representation of the peri-hand space in humans, similarly to that discovered in monkeys by single-cell recording studies (Graziano, 1999; Graziano, Cooke, & Taylor, 2000). These patients are typically impaired in the detection of a contralesional stimulus, delivered in a certain modality (e.g., touch), when an ipsilesional stimulus, delivered in another sensory modality (e.g., vision), is simultaneously presented. Like in unimodal extinction, both the ipsi- and the contralesional stimuli are well perceived when presented in isolation (Heilman, Watson, & Valenstein, 2003). The critical point, here, is that the crossmodal extinction rate of the contralesional tactile stimulus was stronger when the concurrent ipsilesional visual stimulus was presented close to the ipsilesional hand rather than in the far space (di Pellegrino et al., 1997; Elisabetta Làdavas & Farnè, 2004). Furthermore it has been shown that the contralesional tactile stimulus can be extinguished by an ipsilesional visual stimulus presented close to a fake arm (i.e., a realistic prosthesis of a right forearm and hand) mimicking the position of the ipsilesional real arm (Farnè, Pavani, Meneghello, & Làdavas, 2000). Critically, when the posture

of the prosthetic arm was anatomically implausible extinction rate was reduced. This modulation of crossmodal extinction further support the hypothesis of body representation relying on the interactions between visual and somatosensory information related to the body. The strict similitude between these behavioural effects in humans and the modulation of the firing rate of parietal neurons to somatosensory stimuli by the vision of a fake arm in monkeys (Graziano et al., 2000) suggests that it's plausible that the human parietal cortex holds a model of the body. Other studies, in neurologically unimpaired participants, described a speeding up of reaction times to tactile stimuli applied to a body part that was simultaneously seen in a monitor and that might be in the same or different position in respect to the actual position of the real stimulated body part. Interestingly, this effect was even found for body parts which are not directly viewed in normal condition (i.e., the back of the neck; but it has to be noted that the effect was larger for those body parts, such as the face, whose visual experience is more familiar to the participants, for example via self-viewing in a mirror) (Tipper et al., 1998; Tipper et al., 2001a). These results highlight the importance of visual input for the processing of corporeal objects. Other studies emphasize the role of both visual and proprioceptive information for body representation by showing a crossmodal interference effect even using fake arms (Pavani et al., 2000). In other words, a visual object mimicking one's own body part, may actively influence the response to tactile stimuli, supporting the idea that the direct vision of the body may be crucial to shape somatosensory perception. Critically, these authors found interference effects only if the fake hands were in an anatomically plausible position, suggesting that multisensory visuo-tactile integration is truly based on the actual visual input coming from the body. Thus, from a perceptual point of view, it could be supposed that the body receives at least a double encoding (visual and somatosensory-proprioceptive), while any other extrapersonal three-dimensional object is perceived only through the visual modality, unless people actively touch or manipulate it. Thus, the spatial representation of body parts would be not only based on visual input elaborated in a system of egocentric coordinates (namely the absolute position of that bodily unit into the external space), but it would be based, at the same time, on visual and somatosensory input centred on that body part, independently from the

position currently occupied in the external space. In this way the body, would have a richer and more efficient spatial representation, as compared to extracorporeal objects.

A superiority of the spatial representation of body parts, as compared to extracorporeal objects, seems plausible even in the light of the role played by action in imposing a categorical structure on body space. Motor and biomechanical constraints critically segment our body into prototypical functional units (limbs, joints, etc...) that are directly used to reach for objects, implying a precise knowledge about their length and size (de Vignemont, Tsakiris, & Haggard, 2006). Furthermore, the prolonged sensory-motor experience, including the visual observation of the conspecifics, may gradually shapes the so-called body structural description, an explicit visuo-spatial topological map defining the body boundaries and the spatial relationships among different body parts. This representation is supposed to be stored in the left posterior parietal cortex and its damage would be a possible explanation for autotopoagnosia² (Buxbaum & Coslett, 2001; Corradi-Dell'Acqua et al., 2008).

2.2. Visuo-spatial representation of objects

When people look at objects in the external space they are usually immediately able to recognize them, access their semantic representation and assign them a lexical label, as well as localize them in an egocentric system of coordinates (Halligan, Fink, Marshall, & Vallar, 2003). Furthermore, if needed, they can reach for or interact with them. All these cognitive functions imply different mechanisms and, possibly, involve different brain areas (see Fig. 2.1 for a model of object recognition). Ungerleider and Mishkin had hypothesized the existence of two main neural systems representing visual information originating in the striate cortex. The dorsal system, projecting to the posterior parietal cortex, would be responsible for the spatial localization of objects in the extrapersonal space; the ventral system, projecting to the temporal cortex, would be instead responsible for their identification and recognition.

² Autotopoagnosia is defined by the lack of knowledge about the topography of the body. A typical manifestation is the inability to point at a body part on verbal command or imitation.

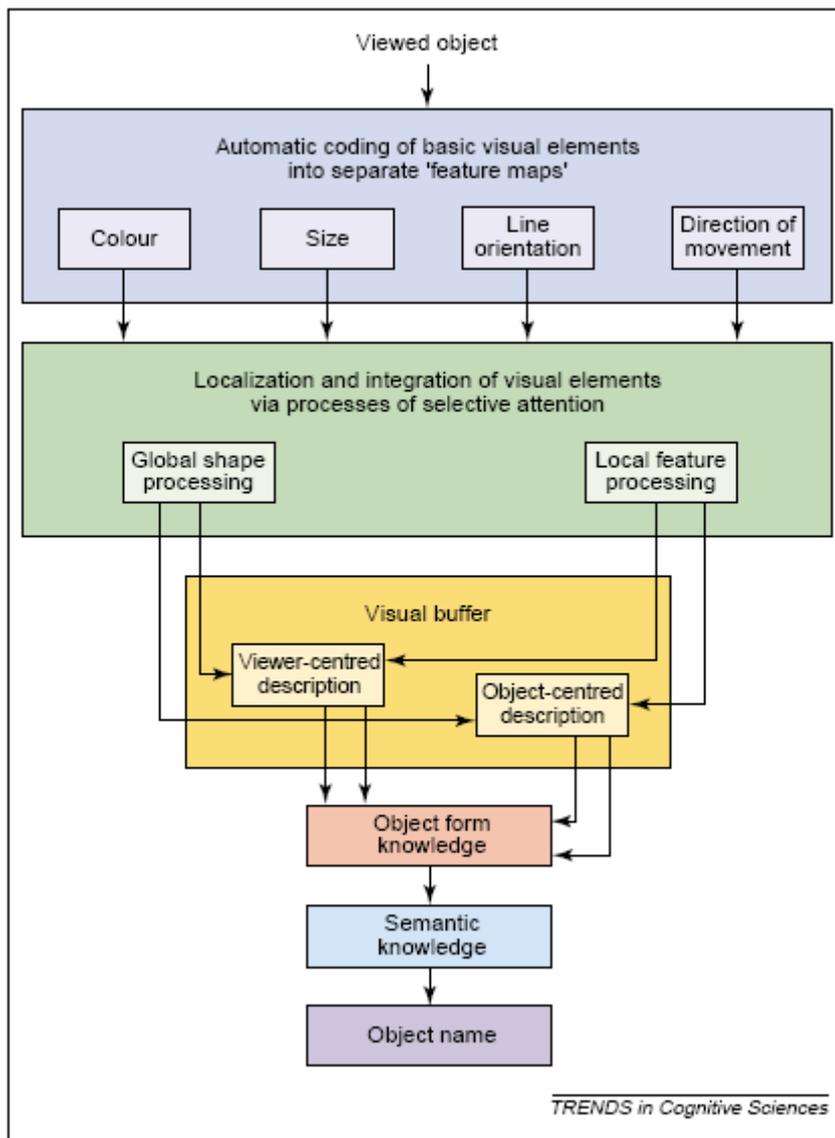


Fig. 2.1

Schematic information-processing model of object recognition (Halligan et al., 2003; with kind permission from Elsevier)

This model has been then reinterpreted by Milner and Goodale suggesting that both the two systems use information about the identity and the spatial location of objects, but in a different way. The dorsal system would be based on egocentric coordinates and thus it would be responsible for the interaction with the objects in the surrounding space; the ventral system would be predominantly implicated in visual recognition processes, but it would provide as well an allocentric representation of the spatial relation within the elements composing the object

and/or among multiple objects (Milner & Goodale, 1995). The existence of these two types of representations (i.e., allocentric and egocentric) is supported, for example, by the dissociation between allocentric and egocentric manifestation of the USN syndrome. Indeed it has been reported the case of neglect patients who, in a copy test, consider only the ipsilesional side of each target stimulus (allocentric neglect), whereas other patients consider only the stimuli placed in the ipsilesional side of the space in front of them (egocentric neglect) (Halligan et al., 2003; Marshall & Halligan, 1993). Once their separate coding is accomplished, egocentrically and allocentrically-referenced sensory information needs to be integrated in a global representation. It has been suggested that in the healthy brain the posterior parietal cortex (PPC) might be a good candidate to fulfil this function. Functional imaging data show increased neural activity in a predominantly right hemispheric fronto-parietal system when healthy participants perform tasks involving the location of a visual stimulus with respect to either their body or another object (Halligan et al., 2003) or the computation of their subjective mid-sagittal plane. In this latter study participants had to press a button when a visual bar, moving from right to left or vice versa, was crossing the mid-sagittal plane of their body. Posterior parietal and lateral frontal premotor region were found active in this experimental condition, with a more extensive activation in the right hemisphere (Vallar et al., 1999).

As mentioned in Section 2.1., the spatial analysis of the length of non corporeal objects may differ from that of bodily segments, due to several reasons, as for example the multiple sensory coding undergone by our own body parts or the existence of an implicit knowledge and representation of body parts size. Indeed objects have a prototypical shape, but they can have different sizes, even an indefinite number in case of objects which are not tools. As an example, a pencil has its standard shape and can be of different lengths within a standard range, whereas a tube has its prototypical cylindrical shape, but it can be built of different length. By contrast body parts hold a stable size in their length and width once people reach adulthood. Thus, arms and legs grow up during infancy and adolescence, but they show a fixed length in healthy adults, with obvious differences between individuals.

In this view, the aim of the first set of experiments reported in this Chapter (Experiments 1 and 2) was to determine whether the body may also undergo a preferential encoding as a spatial object, in respect to other three-dimensional but non-corporeal objects. To this aim a bisection task was used in healthy individual as well as in brain-damaged patients affected by Unilateral Spatial Neglect. The bisection task seemed particularly suitable to this aim, since it typically implies an accurate spatial analysis of the target, being at the same time a sensitive test to the presence of Unilateral Spatial Neglect (see Experiment 2), as briefly illustrated in the next paragraph.

2.3. The bisection task in healthy people and in neglect patients

The task of setting the midpoint of a target, with the target typically being a line, or a gap between two dots, or a three-dimensional object implies an accurate spatial analysis of its length, that is the distance between its endpoints. The bisection of an horizontal segment (line bisection) is widely used, together with other pencil-and-paper tests, to assess the presence of the neglect syndrome (for a standardized version of the test see: (Wilson, Cockburn, & Halligan, 1987). Neglect patients typically displace the subjective midpoint significantly to the right of the veridical centre (e.g., as if they ignore, to a variable extent, part of the left-hand side of the stimulus or as if they are hyperattentive to the right-hand side). Also neurologically healthy subjects often show a systematic bias in this type of task, generally erring to the leftward relative to the veridical midpoint, and thus displaying a phenomenon Bowers and Heilman first referred to as "pseudoneglect" (Bowers & Heilman, 1980). This phenomenon has been shown even in the so-called gap bisection, that is a task in which participants are required to set the midpoint in the empty space between two extremities. In a study by Bradshaw and colleagues subjects were asked to bisect the gap between two LEDs by moving a third LED. The LEDs at the endpoints were manipulated in their flashing rate, brightness and in the timing of the onset and offset. In general participants were found to err more leftward to the objective midpoint, thus showing pseudoneglect, but they also found a bias towards the LEDs that were faint, briefly presented or flashing when the properties of the endpoints were asymmetrically

modified. Another task to assess visuo-spatial abilities is the landmark test in which participants are presented with a bisected line and have to judge if the bisection is made to the left or to the right of the veridical centre. Recent evidence showed that healthy participants tends to overestimate the perceived length of the left side of the lines (i.e., pseudoneglect). In particular Heber and colleagues found a significant leftward bias only when the stimuli were presented in the peripersonal space (Heber, Siebertz, Wolter, Kuhlen, & Fimm, 2010)

As Jewell and McCourt noticed in their meta-analysis (Jewell & McCourt, 2000), pseudoneglect is actually a less consistent phenomenon if certain variables are taken into account; thus, as example, age is a conditioning factor (with older subjects often erring rightward and thus not showing any pseudoneglect) as well as the hand used to perform the task (with subjects often displacing the midpoint towards the side of the hand used as effector). In general they highlight the fact that *"if some subjects make consistent leftward bisection errors while others make consistent rightward errors, the proportions of these so-called 'left-shifters' and 'right-shifters' selected in a particular experiment would largely determine its results (p.95)"*.

All the experiments reported in this thesis have compared participants' performance in more than one bisection condition using a "repeated measure rationale" and thus avoiding, or at least restricting, the problem of individual differences. In other words, the critical comparisons have been always made between conditions and not between participants so that the proportions of 'left or right-shifters' selected did not influence the results and their interpretation.

2.4. Experiment 1

Experiment 1, starting from the literature showing that it's plausible to hypothesize a sort of superiority of the body representation over the spatial representation of any other extracorporeal object, investigates the possibility that Unilateral Spatial Neglect (USN) may affect to a different extent the spatial analysis of body parts relative to extrapersonal three-dimensional objects. Patients affected by USN, usually affected by a right hemisphere lesion, show an altered representation of the contralesional left side of space. They typically fail to perceive, pay attention or act towards contralesional stimuli as well as to represent the contralesional side of the space (Bisiach & Vallar, 2000; Heilman et al., 2003; Husain, 2008; Karnath, Milner, & Vallar, 2002). In line bisection tasks, which is one of the tests used to evaluate the presence of the USN, neglect patients typically displace the subjective midpoint towards the right side to a variable extent, as compared to the objective midpoint (see e.g., (Bisiach, Bulgarelli et al., 1983; Halligan & Marshall, 1988; Heilman & Valenstein, 1979).

Unilateral Spatial Neglect is not a unitary syndrome, since it can affect different aspects of spatial representation in a dissociate manner. So, for example, it can be limited to the egocentric versus allocentric spatial coordinates system (Halligan et al., 2003). Another critical dissociation is that between extrapersonal and personal space, with the patient being compromised in representing, using or paying attention to either the contralesional left-sided space or body parts. USN for extrapersonal space without any sign of personal neglect is actually more frequent, even if also the opposite case has been described (see patient E.D.S. in (Guariglia & Antonucci, 1992).

Most of the studies investigating the bodily aspects of the neglect syndrome have focused mainly on personal neglect (Bisiach, Perani, Vallar, & Berti, 1986; Guariglia & Antonucci, 1992), motor neglect (Castaigne, Laplane, & Degos, 1972; Heilman, 2004), anosognosia for neurological deficits (Berti et al., 2005; Bisiach, Vallar, Perani, Papagno, & Berti, 1986; Pia, Neppi-Modona, Ricci, & Berti, 2004) and delusional views (such as somatoparaphrenia, (Vallar & Ronchi, 2009) concerning the contralesional side of the body. However there is lack of information about any possible impairment of the spatial metric of body parts in USN. In

particular, in spite of the rich body of evidence related to the bisection of extrapersonal objects and the inclusion of a test of line bisection in standard pencil-and-paper batteries for USN (e.g., (Wilson et al., 1987), no information is available about the bisection of body parts. Thus, in order to address this issue, Experiment 1 investigates the possibility that bodily segments may be, or not, affected by USN as any other object holding a physical extension in space³. Thus, patients were asked to bisect their left forearm and a length-matched cylindrical object with their unimpaired right dominant hand.

2.4.1. Materials and methods

2.4.1.1. Participants

Participants were recruited from the inpatient population of two Neurological Rehabilitation Units (U.O. Riabilitazione Neuromotoria, P.R.M. Bozzolo, Mantova, Italy; IRCCS Istituto Auxologico Italiano, Milano, Italy). All participants gave their informed consent to take part in the study according to the Declaration of Helsinki (BMJ 302 (1991) 1194). Fourteen right-handed volunteers (11 males and 3 females; mean age: 69; mean educational level: 9 years), with no history or evidence of neurological disease and fourteen right-handed right-hemisphere-damaged patients (11 males and 3 females; mean age: 66; mean educational level: 9 years) participated in the study. For the patients' group, inclusion criteria were the presence of left unilateral spatial neglect (USN), as assessed by a standard battery (see below) as well as the presence of a unilateral brain lesion. All patients had no history or evidence of neurological and/or psychiatric disorders. Contralesional motor, somatosensory and visual field deficits, including extinction to tactile and visual stimuli, were assessed by a standard neurological examination (Bisiach, Cappa, & Vallar, 1983). Anosognosia was also assessed in the motor, somatosensory and visual domain (score range: 0 = unimpaired performance; 3 = maximum deficit) (Bisiach, Vallar et al., 1986). Table 2.1 provides detailed demographical and clinical neurological data for each patient.

³ A further hypothesis of a positive correlation between personal neglect and the extent of the deviation error in the forearm bisection could not be tested because no patient showed signs of personal neglect.

| | Length of illness (days) | Age/ gender | Aetiology | Neurological examination | | | Anosognosia | | |
|-----|-----------------------------|-------------|-----------|--------------------------|-----|-----|-------------|----|---|
| | | | | V | SS | M | V | SS | M |
| P1 | 75 | 71/M | I | + | + | + | 2 | 2 | 3 |
| P2 | 36 | 59/M | I+H | + | + | + | 0 | 0 | 0 |
| P3 | 37 | 50/M | H | + | + | + | 2 | 2 | 0 |
| P4 | 83 | 80/F | I | + | + | + | 2 | 0 | 2 |
| P5 | 44 | 62/F | I | + | + | + | 2 | 3 | 3 |
| P6 | 43 | 76/M | I+H | + | + | + | 3 | 3 | 0 |
| P7 | 22 | 68/M | I | + | + | + - | 3 | 0 | 0 |
| P8 | 35 | 76/M | I | ext | ext | + | 0 | 0 | 2 |
| P9 | 35 | 57/M | I | - | - | + - | 0 | 0 | 0 |
| P10 | 28 | 60/M | I | ext | + | + | 0 | 0 | 0 |
| P11 | 38 | 35/M | A | + | + | + | 3 | 3 | 0 |
| P12 | 44 | 76/M | I | - | ext | + | 0 | 0 | 0 |
| P13 | 72 | 53/F | I | + | + | + | 0 | 0 | 0 |
| P14 | 38 | 85/M | I | + | - | + | 0 | 0 | 0 |

Tab. 2.1 Demographical and clinical data about neurological deficit of the patients

Aetiology: I/H/A=ischaemic/haemorrhagic/aneurysm.

Neurological examination: V/SS/M = visual/somatosensory/motor deficits contralateral to the damaged hemisphere; + = present; - = absent; +- = minor deficit; ext = extinction to double simultaneous stimulation.

A mapping of brain lesions is provided in Fig. 2.2, for the nine out of fourteen patients for whom a brain scan was available. The extension and localization of the lesions were quite different among the patients, involving various parts of the dorso-lateral-fronto-temporo-parietal cortices, the insula as well as the subcortical white matter and the basal ganglia, while sparing the occipital cortex (Fig. 2.2).

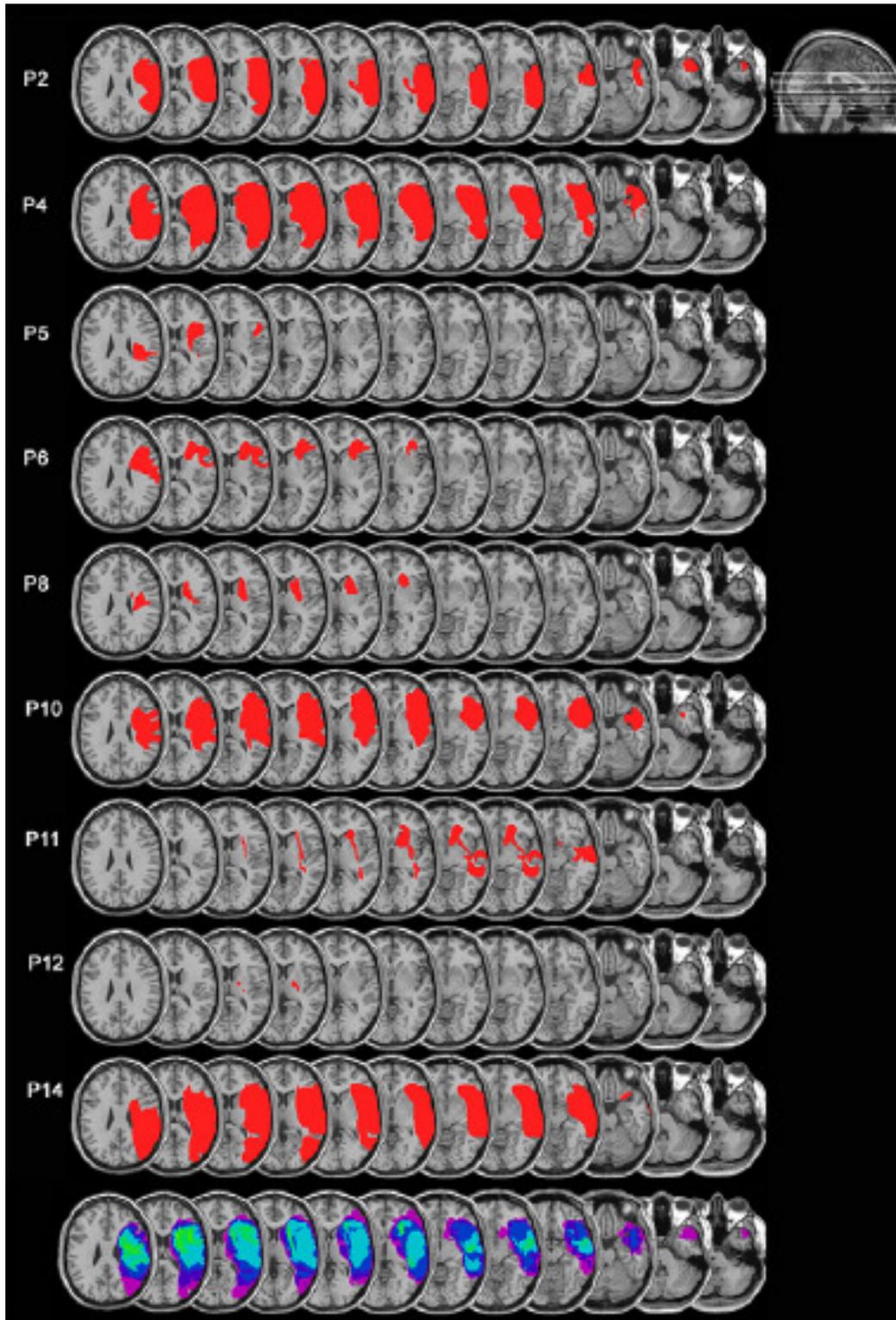


Fig. 2.2

Lesion mapping. Lesions were mapped onto a standard template (Montreal Neurological Institute) using the software MRICro (Rorden & Brett, 2000). Red areas represent the extension of the lesion of each single patient. In the bottom row the area of lesion overlap is shown: yellow-green areas indicate maximum overlap; pink areas indicate minimum overlap.

2.4.1.2. Neuropsychological battery for extra-personal and personal USN

2.4.1.2.1. Extra-personal USN

(a) Cancellation tasks: Line (Albert, 1973); Letter (Diller & Weinberg, 1977; Vallar, Rusconi, Fontana, & Musicco, 1994); Star (Wilson et al., 1987).

(b) Bisection of six horizontal lines (10, 15, 25 cm long; 1 mm wide). For each bisected line, the length of the left half was measured at the nearest millimetre and a *percentage deviation score* was calculated by means of the same formula as in Experiment 1: $[(\text{measured left half} - \text{objective left half}) / \text{objective left half} * 100]$ obtaining positive values for rightward deviations and negative values for leftward deviations. Control data for this version of the line bisection task were collected from 15 neurologically unimpaired volunteers (8 males and 7 females; mean age: 66; mean educational level: 6 years). The mean percentage deviation score of the control group was +0.47% (s.d. +/- 2.72, range: -5.4%/+4.8%). Cut-off was 2 standard deviation above/below the mean percentage deviation of controls, so any percentage deviation score higher than 5.91% was considered abnormal.

(c) Drawing tests

(1) Clock drawing: Patients were required to place the 12 hours in a circle drawn on an A4 sheet and draw the clock hands on the 11.10 position. Each drawing was scored as follows: (i) *completeness of the clock face numbers* (score range: 0= more than two number missing; 1= additional numbers; 2= two or less number missing; 4= all the numbers are present); (ii) *spatial arrangement of the numbers* (score range: 0= completely incorrect spatial arrangement; 2= minor displacement (less than 15° and lack of the 3/9 and 6/12 axes ; 3= symmetrical positioning of the elements in the two halves of the clock and regular distance between the numbers); (iii) *hour hands* (score range: 0= hands missing or highly displaced; 1= minor displacement; 2.5= correctly placed); (iv) *an additional score* of 0.5 was added if the two hands were correctly drawn of different lengths. The total score range was 0 (maximum impairment) to 10 (unimpaired performance).

(2) Copy of a complex line drawing: Patients were asked to copy a line drawing comprising five objects (two trees on the left and two on the right-hand side and a house at the centre, between the trees; (Gainotti, Messerli, & Tissot, 1972). A qualitative scoring was used: correct copies of each figure element was scored 1 for the trees and 2 for the house. The lack of any single element of each tree determined a score of 0. For the house, the lack of single elements or perspective was scored 1, any further error was scored 0. The total score range was 0-6. the patients' errors consisted in the omission of left-sided objects or of left-sided details of one or more items.

(d) Sentence reading (Pizzamiglio et al., 1992): Patients were asked to read five sentences. The score was the number of correctly read sentences (range: 0-5). Neurologically unimpaired participants and patients with right-side brain lesion without USN make no errors on this test.

2.4.1.2.2. Personal USN

(a) Fluff test (Cocchini, Beschin, & Jehkonen, 2001): Patients, blindfolded, were required to reach with the right ipsilesional hand for 24 targets located on the right-hand (9 items: three on the arm; three on thigh; three on the leg) and on the left-hand (15 items: three on the arm; three on the forearm; three on the torso; three on thigh; three on the leg) side of their body relative to the midline. The number of collected items on both sides was scored (range 0-9 on the right; 0-15 on the left side of the body; cut-off: 13/15 on the left side), for a total maximum score of 24. For patients #1, #3 and #13, who were unable to reach their leg due to motor impairment, the three lowermost targets on the leg were not applied on both sides.

(b) Touching the contralesional hand with the ipsilesional hand (score range: 0= unimpaired performance; 3= maximum deficit; (Bisiach, Perani et al., 1986).

Patients' performances in each test are reported in table 2.2

| | Line bisection (%) | Line cancellation | | Letter cancellation | | Star cancellation | | Drawing | | Reading | Fluff test | | Personal neglect |
|-----|--------------------|-------------------|--------|---------------------|--------|-------------------|--------|---------|---------|------------|------------|-----|------------------|
| | | L | R | L | R | L | R | Copy | Clock | | L | R | |
| P1 | 24.8* | 0/18* | 8/18* | 0/53* | 8/51* | 0/30* | 9/26* | 0/6* | 0/10* | 0/5* | 10/12* | 3/6 | 0/3 |
| P2 | 83.2* | 0/18* | 12/18* | 0/53* | 6/51* | 0/30* | 10/26* | 0/6* | 6.5/10* | 0/5* | 15/15 | 9/9 | 0/3 |
| P3 | 20.6* | 17/18* | 18/18 | 1/53* | 32/51* | 6/30* | 25/26 | 0/6* | 4/10* | 3/5* | 8/12* | 5/6 | 0/3 |
| P4 | 19.6* | 13/18* | 18/18 | 0/53* | 11/51* | 0/30* | 14/26* | 3/6* | 4/10* | 0/5* | 15/15 | 8/9 | 0/3 |
| P5 | 3.4 | 1/18* | 18/18 | 44/53* | 49/51 | 22/30* | 26/26 | 2/6* | 0/10* | 5/5 | 15/15 | 9/9 | 0/3 |
| P6 | 3.4 | 18/18 | 18/18 | 45/53* | 47/51 | 22/30* | 26/26 | 5/6* | 9.5/10 | 4/5* | 0/15* | 0/9 | 0/3 |
| P7 | 15.4* | 18/18 | 18/18 | 36/53* | 50/51 | 20/30* | 26/26 | 3/6* | 3/10* | 4/5* | 14/15 | 8/9 | 0/3 |
| P8 | 12.6* | 18/18 | 18/18 | 49/53 | 48/51 | 29/30 | 25/26 | 0/6* | 0/10* | Illiterate | 2/15* | 3/9 | 0/3 |
| P9 | 12.4* | 18/18 | 18/18 | 34/53* | 51/51 | 30/30 | 25/26 | 6/6 | 8.5/10* | 5/5 | 8/15* | 4/9 | 0/3 |
| P10 | 1.8 | 17/18* | 18/18 | 39/53* | 51/51 | 27/30 | 26/26 | 3/6* | 9.5/10 | 5/5 | 14/15 | 9/9 | 0/3 |
| P11 | 11.2* | 13/18* | 18/18 | 0/53* | 14/51* | 0/30* | 12/26* | 2/6* | 4/10* | 0/5* | 15/15 | 8/9 | 0/3 |
| P12 | 17* | 17/18* | 18/18 | 47/53* | 49/51 | 28/30 | 25/26 | 4/6* | 6/10* | 5/5 | 15/15 | 9/9 | 0/3 |
| P13 | 11.2* | 15/18* | 18/18 | 2/53* | 35/51* | 0/30* | 14/26* | 0/6* | 1/10* | 4/5* | 3/12* | 3/6 | 0/3 |
| P14 | 27.2* | 18/18 | 18/18 | 44/53* | 46/51* | 22/30* | 24/26 | 0/6* | 0/10* | 2/5* | 11/15* | 9/9 | 0/3 |

Tab. 2.2 Neuropsychological baseline assessment for unilateral spatial neglect

Line bisection: percentage of rightward deviation error. Cancellation tests and Fluff test: target detected in the left- and right-hand sides of the sheet (L/R).. Drawing, reading and personal neglect tests: patient's score/maximum possible score. Asterisks and bold indicate a defective score.

2.4.1.3. Experimental Procedure

Participants sat on chair and were presented with a stimulus placed at approximately 20 cm from the body, with the objective midpoint aligned with their midsagittal plane. The stimulus could be either their own left forearm (Forearm condition) or a plastic cylinder (Solid condition). The stimulus was placed on a wooden board with a black pipe fixed at its right extremity. Before starting the experiment, for each participant, the length of cylinder was exactly matched to that of the participant's forearm, as measured between the proximal and distal extremities of the ulnar bone. In order to do so, the right extremity of the cylinder was hidden into the black pipe described above, so that the remaining visible part matched the length of the forearm (Fig. 2.3 A). During the Forearm condition the left hand was placed into the masking pipe so that only the forearm remained visible (Fig. 2.3 B). This was done in order to avoid that the hand, which is the most salient part of the arm, could exert any attention-grabbing effect, thus biasing *per se* the bisection.

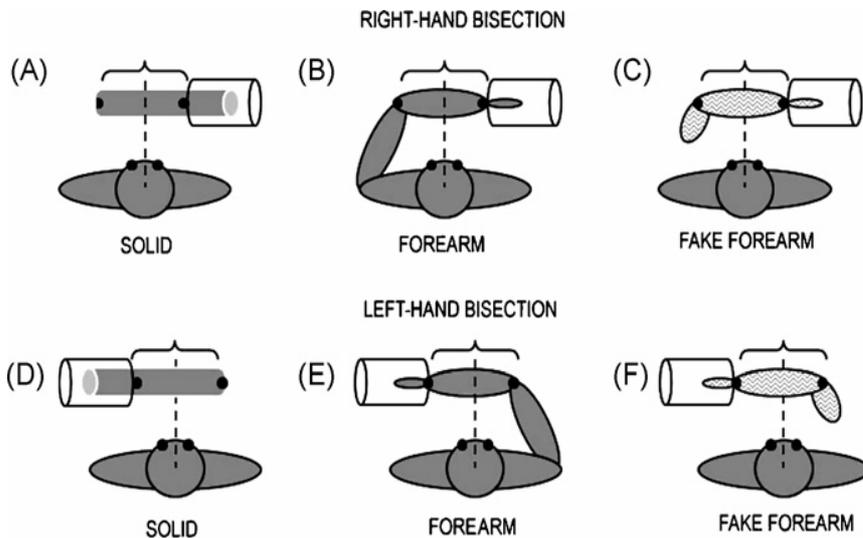


Fig. 2.3

Schematic bird's eye view of the experimental setting. In Experiment 1 only the conditions depicted in panels A and B were used, while all the conditions were used in Experiment 2. The cylinder shown at the right (panels A-B-C) or left (panels D-E-F) end of the solid and forearm stimuli was opaque in the real experimental setting in order to hide the hand and equate the length of the solid to that of the participant's forearm.

In each condition the right and the left extremities of the stimulus were marked by black tags and clearly indicated to the participant prior to each block of trials. Participants rested their right index finger touching the body midline and, following a vocal command given by the experimenter, were required to point to the midpoint of the stimulus considering the black tags as its right and left endpoints. After each pointing, performed with no time constraints and no corrections allowed, the experimenter measured, at the nearest millimetre, the distance between the left side of the stimulus and the point indicated by the participant. The participant was then required to put the index finger back to the starting position. There were 24 trials for each stimulus condition (i.e., 24 forearm bisections and 24 solid bisections). The total of 48 trials were equally distributed in four block of 12 trials each, following an ABBA design. Half of the participants started with the Forearm condition and the other half with the Solid condition. In order to avoid stereotyped motor responses during the task, in each block a separate line bisection task was interspersed every 4 trials. In this condition, participants were asked to set the midpoint of four segments (5 cm long, 1 mm wide), horizontally aligned on an A4 sheet, pointing with their right or left index finger. The results of these bisections were not further considered for analysis. A *percentage deviation score* was calculated for each condition by means of the following formula: $[(\text{measured left half} - \text{objective left half}) / \text{objective left half} * 100]$. This transformation yields positive values for rightward deviations and negative values for leftward deviations. The mean percent deviation scores were analyzed by a mixed design analysis of variance (ANOVA) with a between-subjects factor Group (Control participants, USN patients) and a within-subjects factor Stimulus (Solid, Forearm).

2.4.2. Results

Fig. 2.4 shows that USN patients made a larger average bisection error than neurologically unimpaired participants. In the patients' group the error was towards the right side in both the conditions, consistently with the spatial defect brought about by the neglect syndrome, while in the control group the error was rightward in the Solid condition and slightly leftward in the Forearm condition. More interestingly, both the groups showed a smaller error in the forearm

bisection compared to the cylinder bisection. The ANOVA revealed a significant effect of Group [$F(1,26)=15.5$; $p<0.01$, $\eta^2=0.37$]: USN patients showed a greater rightward bisection error than control (mean deviation score: 15.90% vs. 0.89%). A significant main effect of Stimulus condition was also found [$F(1,26)=13.5$; $p<0.01$, $\eta^2=0.34$], showing that in both the groups the estimation of the subjective midpoint of the forearm was significantly more accurate than that of the solid (mean deviation score: 5.08% vs. 11.70%). The Group by Stimulus interaction did not reach any significant level [$F(1,26)=0.4$; $p=n.s.$, $\eta^2=0.01$].

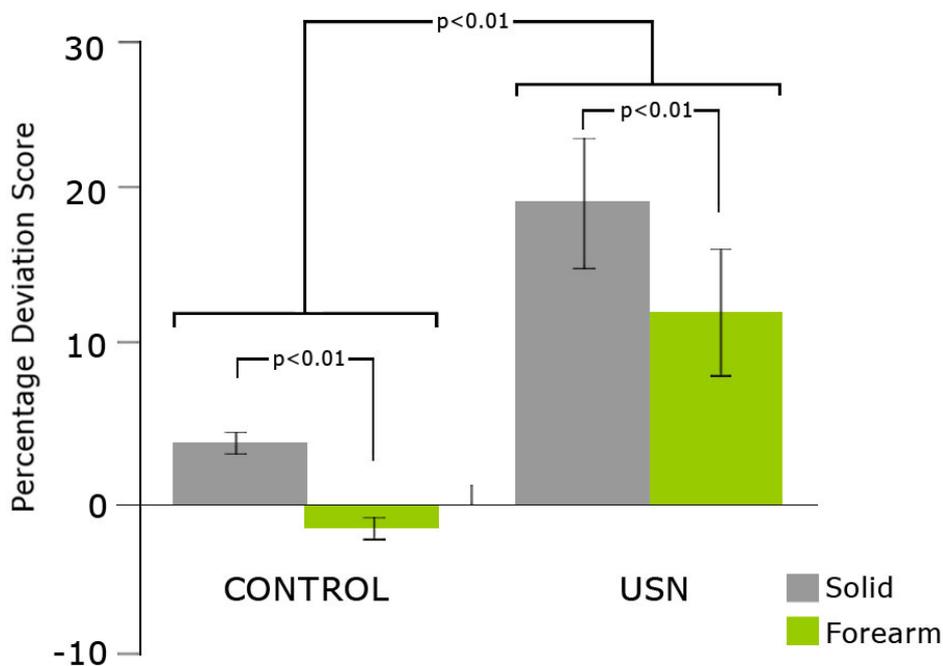


Fig. 2.4 Mean percent deviation score.

Mean percent deviation error (\pm standard errors) in neurologically unimpaired participants and in neglect patients in the two bisection conditions (Solid: grey columns; Forearm: green columns).

Additionally it has been compared the performance of each patient in the two conditions with the same performance in the control group. To this aim t-tests were performed following the procedure by Crawford and Garthwaite (Crawford & Garthwaite, 2005). All but three patients (#5, #10 and #14) showed some degree of difference in the amount of error in one or both bisection conditions, as compared to the control group ($p<0.01$ for all comparisons, see Fig.

2.5). Furthermore, using the Revised Standardized Difference Test (Crawford & Garthwaite, 2005), the difference between solid and forearm bisection in each patient was compared with the same difference in the neurologically unimpaired participants. Four patients showed a significant difference between the two experimental conditions consisting in an advantage for the forearm bisection as compared to the solid bisection (difference in the deviation score between the two conditions: patient #2: 21.9%, $t(13)=3.627$; $p<0.01$; patient #8: 31.7%, $t(13)=5.738$; $p<0.001$; patient #11: 26.01%, $t(13)=4.512$; $p<0.001$; patient #12: 20.7%, $t(13)=3.355$; $p<0.01$). Two patients showed an opposite advantage in the solid bisection (patient #6: 9.3%, $t(13)=-3.251$; $p<0.01$; patient #7: 5.73%, $t(13)=-2.461$; $p<0.05$). Furthermore, patient #11 exhibited an impairment only in solid bisection, as compared to the control group, with the performance in the forearm bisection being within the normal range (Solid: 23.2%, $t(13)=6.742$; $p<0.01$; Forearm: -2.85%, $t(13)=-0.376$; $p=n.s.$) (see Fig. 2.5 for details).

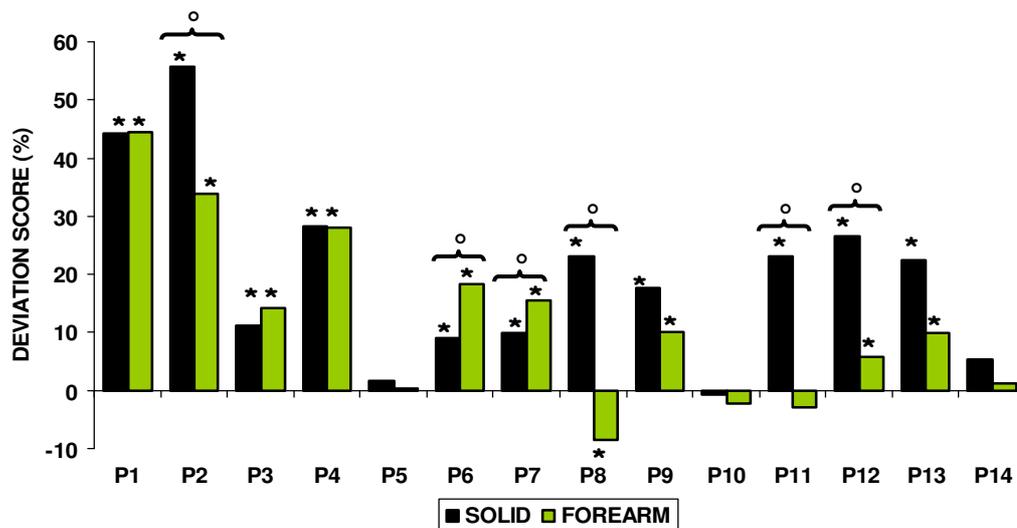


Fig. 2.5 Mean percent deviation score by stimulus condition in the 14 USN patients.

Asterisks indicate a significant difference between each patient's performance and the same performance in the control group. Circles indicate a significance difference between solid and forearm bisection in the individual patient, as compared to the same average difference in the control group.

These single-case analyses show that in different patients the deficit may involve mainly the solid bisection (i.e., the prevailing pattern) or the forearm bisection.

2.4.3. Discussion

Right-brain damaged patients with left USN bisected overall more accurately their own left forearm, than a size-matched three-dimensional object placed at the same spatial location. Also in neurologically unimpaired participants the bisection error was smaller in the forearm condition than in the solid condition. Thus, it can be suggested that the representation of the length of body parts shows a consistent advantage as compared to that of extrapersonal objects. The predominant pattern of an advantage in the coding of the length of body parts relative to extracorporeal objects might depend upon the fact that body representation is supported by multisensory (visual and somatosensory-proprioceptive) codes (di Pellegrino et al., 1997; Elisabetta Làdavas & Farnè, 2004; Maravita et al., 2003; Tipper et al., 2001b) that, in their somatosensory-proprioceptive components are not available to extracorporeal objects. Nevertheless, it seems also plausible that the visual appearance of the forearm, as a highly specific and familiar object, may play a critical role, activating, for instance, a prototypical visuo-spatial shape of one's own forearm, resulting in a more accurate spatial encoding. The vision of a body part may activate its prototypical standard representation, including information about its size and length (de Vignemont, 2010; de Vignemont et al., 2006; Longo, Azanon, & Haggard, 2010; Taylor-Clarke, Jacobsen, & Haggard, 2004). This would result in a more accurate computation of the spatial metrics of body parts and, thus in a better bisection performance in healthy participants and a reduced USN bias in the patients. Experiment 2, presented in the next session, further examined this issue.

Notwithstanding the general advantage for the spatial analysis of bodily as compared to non corporeal objects, a more detailed analysis of the performance within the neglect group showed a tendency for a double dissociation between body parts' and objects' bisection. As compared to neurologically unimpaired participants, four out of fourteen USN patients exhibited a smaller rightward deviation in the forearm bisection relative to the cylinder bisection, while two patients showed the opposite pattern, with an advantage in the Solid condition. While definitive conclusions concerning the anatomo-clinical correlation of this double dissociation cannot be drawn due to the small number of relevant patients, it may be noted that the lesions of patients

showing any dissociation in the two bisection tasks spare area EBA (see Fig. 2.6) (Talairach coordinates 51, -71, 1; (Talairach & Tournoux, 1988), according to Downing et al. (2001). This finding suggests that the double dissociation between solid and forearm bisection may arise from the selective impairment of networks concerned with the spatial representation of objects and body parts, located more anterior with respect to EBA, possibly involving fronto-parietal structures, which are critical to many aspects of spatial cognition and body knowledge (e.g., (Vallar & Maravita, 2009).

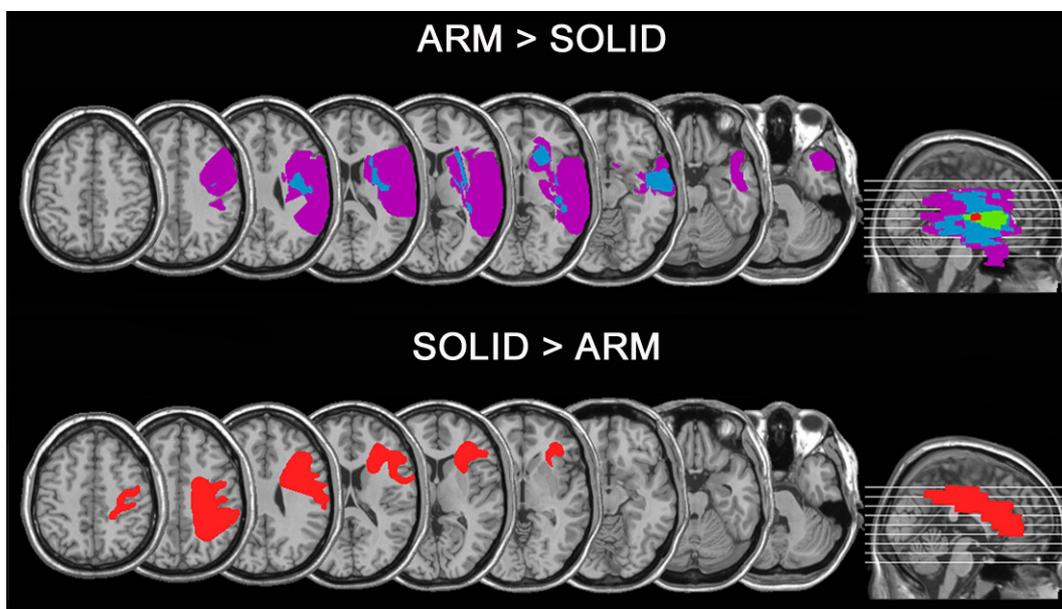


Fig. 2.6

Lesion reconstruction of patients showing an advantage in the forearm bisection (patients #2, #8, #11, #12; lesions involved the precentral, inferior frontal, postcentral, supramarginal superior and middle temporal gyri, insula, caudate, putamen and the surrounding white matter) or an advantage in the solid bisection (patients #6; lesion involved the precentral, inferior frontal, postcentral, inferior parietal and insular cortex and the surrounding white matter).

Finally, no reliable association was found between a deficit in the bisection of the forearm and personal neglect. Patients with personal neglect fail to reach for their contralesional limbs and typically do not use them (Bisiach, Perani et al., 1986; Guariglia & Antonucci, 1992). This condition is believed to reflect a disrupted representation of the contralesional side of the body and, as mentioned in Section 2.4., can be dissociated from extrapersonal neglect. The two

patients (#6 and #7) displaying an higher impairment in the forearm than in the cylinder bisection showed a preserved performance in the test for personal USN (Bisiach, Perani et al., 1986). Patient #6 reported a defective score in the Fluff Test, although with no difference between the left and the right side of the body and thus suggesting a general non-lateralized difficulty in performing the task, probably unrelated to personal USN. By contrast, patients #1, #3, #8, #9, #13 and #14, exhibiting an advantage for the forearm over the solid bisection, showed no personal neglect in the test by Bisiach et al. (1986), but some degree of impairment in the Fluff test (although, even in this case, it was mostly a bilateral deficit). These findings suggest, therefore, that the ability to reach for contralesional body parts, typically affected by personal neglect, and the representation of their spatial extent, as indexed by a bisection task, are dissociable functions.

2.5. Experiment 2

Results from Experiment 1 support the idea that discrete and independent mechanisms may control the spatial processing of the length of corporeal relative to extracorporeal objects, with the former having a more stable metric representation.

In Experiment 2 neurologically unimpaired volunteers performed the task on three different target conditions (real forearm, fake forearm and cylinder) using alternatively the right or the left index finger to indicate the subjective midpoint. This procedure made it possible to compare between the different mechanisms underlying the spatial processing of extrapersonal three-dimensional objects and body parts. The working hypothesis was to find a superiority for the spatial analysis of body parts as compared to extra-corporeal objects. Furthermore, it was investigated whether any possible difference in the spatial coding of real and fake body parts could be mainly due to a richer sensory input from the body, or to the prototypical shape of bodily segments.

2.5.1. Materials and methods

2.5.1.1. Participants

Twelve right-handed neurologically unimpaired participants (6 females and 6 males; mean age: 62; educational level: 13 years) took part in the experiment. All the volunteers gave their informed consent according to the Declaration of Helsinki (BMJ 302 (1991) 1194).

2.5.1.2. Experimental procedure

Participants sat on a chair and were presented with a stimulus in front of them, placed at a distance of about 20 cm from the starting position of the hand used for the bisection task, with the objective midpoint aligned with their midsagittal plane. They were required to set the midpoint: (a) of their left forearm, a left-sided fake-forearm and a cylinder (having the same length as the participant's forearm) using their right index finger (Fig. 2.3 A-C); (b) of their right forearm, a right-sided fake-forearm and a cylinder with the left index finger (Fig. 2.3 D-F). As in Experiment 1, the hand (belonging to the real or the fake forearm) and the spatially

correspondent extremity of the cylinder (the right-hand side, or the left-hand side, depending on the forearm orientation) were hidden inside the black pipe fixed at one extremity of the wooden board on which the stimuli were placed. The experimental procedure within each block of trials was the same as in Experiment 1. Half of the participants started with bisections performed with the right hand and the other half with the left hand. With each hand participants performed 24 bisection trials in each stimulus condition (i.e., 24 for the Solid, 24 for the Forearm and 24 for the Fake-Forearm). The 72 trials were distributed in 6 blocks, each including 12 trials (i.e., two blocks for each condition), following an ABC-CBA design. There were six possible block orders, randomly assigned to the six participants starting with the right hand and to the six ones starting with the left hand (ABC-CBA, ACB-BCA, BAC-CAB, BCA-CBA, CAB-BAC, CBA-ABC). Once participants had completed the task with one hand, they started with the other one following the same block order, so that the total number of bisections was 144 for each participant. The standardized deviation score used in Experiment 1 was computed and used as dependent variable for statistical analyses. A within-subjects ANOVA was performed with the following factors: Stimulus (Solid, Forearm, Fake Forearm) and Bisecting Hand (Right, Left).

2.5.2. Results

Fig. 2.7 shows that participants made overall leftward bisection errors on the real and the fake forearm, with either hands. By contrast, in the Solid condition, participants made a rightward error with right hand and a leftward error with the left hand. The main effect of the Stimulus [$F(2,10)=0.6$; $p=n.s.$, $\eta^2=0.006$] and Bisecting Hand [$F(1,11)=4.4$; $p=n.s.$, $\eta^2=0.09$] factors were not significant, whereas the Stimulus by Bisecting Hand interaction was significant [$F(2,10)=20.9$; $p<0.001$, $\eta^2=0.4$]. Post hoc Newman-Keuls multiple comparisons showed a significant difference between Solid and Forearm (right bisecting hand: mean deviation 3.65% vs. -3.1%; $p<0.01$; left bisecting hand: -8.5% vs. -3.6%; $p<0.01$) and Solid and Fake-Forearm (right bisecting hand: 3.65% vs. -4.2%; $p<0.01$; left bisecting hand: -8.51% vs. -0.88%;

$p < 0.01$), while there was no difference between Forearm and Fake-Forearm (right bisecting hand: -3.1% vs. -4.2% ; $p = 0.7$; left bisecting hand: -3.6% vs. -0.88% ; $p = 0.2$). Furthermore, a right vs. left bisecting hand difference was found only in the Solid condition (mean: 3.65% vs. -8.51% ; $p < 0.01$), but neither in the Forearm (mean: -3.1% vs. -3.6% ; $p = 0.7$) nor in the Fake-Forearm (mean: -4.2% vs. -0.88% ; $p = 0.2$) conditions.

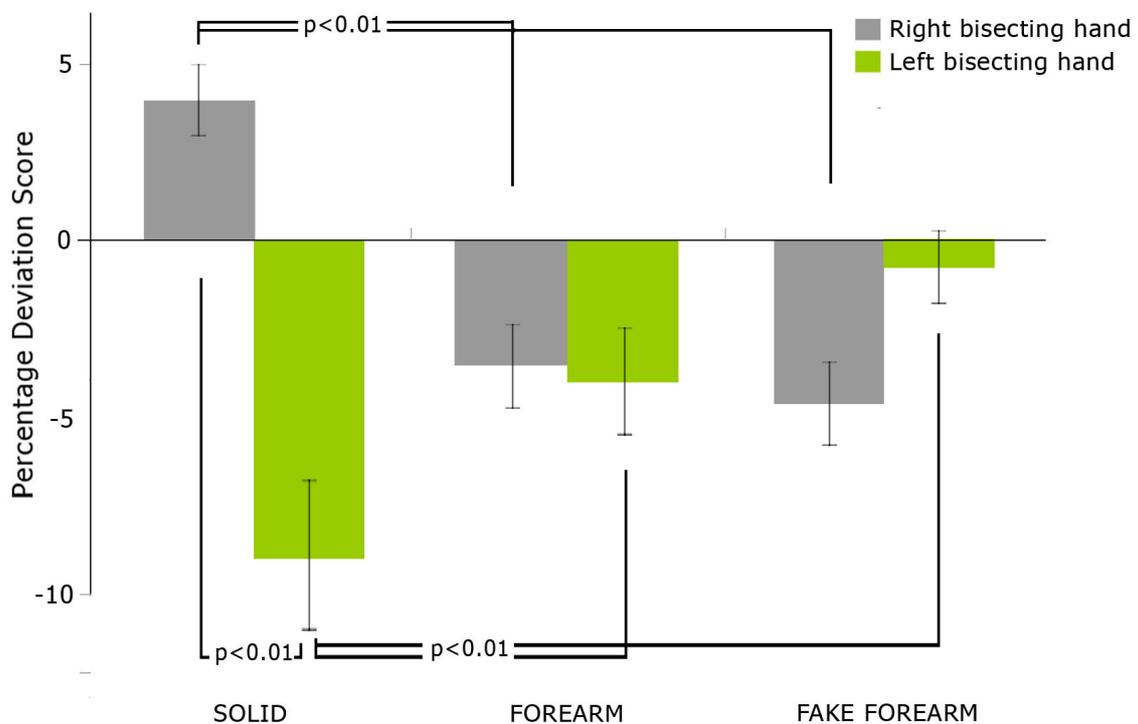


Fig. 2.7 Mean percent deviation score.

Mean percent bisection error in the three bisection conditions (Solid, Forearm and Fake Forearm) performed with the right (grey columns) or left (green columns) hand.

Overall the main finding of this experiment is that the bisection performed on a real or a fake forearm produce a similar amount and direction of error relative to the same task performed on a cylinder, thus suggesting a similar kind of spatial analysis for corporeal objects, either real or fake, relative to non-corporeal objects.

2.5.3. Discussion

These results support the idea that discrete and independent mechanisms may control the representation of the length of body parts, as compared to extrapersonal objects. Since no differences have been found between the spatial analysis of real and fake body parts, it can be suggested that the spatial processing of body parts critically depends upon their prototypical visuo-spatial shape (de Vignemont, 2010; Longo et al., 2010). Similarly to the study by Pavani and colleagues (Pavani et al., 2000), in which the vision of a fake hand close to the visual distractors enhances their interference effect on the tactile stimuli delivered to the real hand, it seems here that the vision of a bodily segment, either real or fake, may activate its standard representation, allowing the participant to refer to a sort of template including spatial information about its length and thus making the two "bodily object" conditions similar to one another. Additionally, the performance showed to be independent from the hand used to perform the task in the Forearm and Fake-Forearm conditions, but not in the Solid condition, suggesting the existence of a quite stable metric representation of body parts that would act as a reference point, making the performance not open to the influence of external variables, such as the performing hand. Indeed, as shown by the performance in the Solid condition, performing the task with the non-dominant hand might be more difficult than perform it with the dominant one. Critically, however, when the target of the task was a body part, such external factors seem to not affect the performance. Furthermore, the Solid condition was the only one displaying a significant tendency in displacing the midpoint towards the side of the hand used to perform the task, as reported by several studies which have investigated the role of the effector on the direction of the line bisection bias (Jewell & McCourt, 2000). Again, the fact that this difference was not found in the Forearm and Fake Forearm conditions may be taken as evidence of the existence of a more stable metrics of body parts, as compared to extrapersonal objects, which seems to be less prone to be influenced by external factors.

Taking together the results of these two experiments it seems that body parts, either real or fake, show a similar advantage in their spatial analyses, relative to extracorporeal objects. Thus, it is conceivable that for the present bisection task, the role of ongoing somatosensory

information coming from the arm is less critical than in other experimental conditions. This may be true especially for the limbs, which are the actual effectors by means of which people move, reach for objects and, more generally, act in the external environment (see for a discussion (de Vignemont et al., 2006). In particular, other tasks that involve the spatial localization of somatosensory stimuli on the skin or visual stimuli nearby the body may critically benefit of proprioceptive information signalling the body posture (Botvinick & Cohen, 1998; Lackner, 1988; Pavani et al., 2000; C. Spence et al., 2008). The present results more likely suggest that a quite stable metric representation of body parts is available to the brain, partially independently from ongoing sensory information. Or it could also be the case that the direct vision of a body part, either real or fake, automatically activate the above mentioned metric representation rendering the task partially independent from other somatosensory information. Indeed this type of information have been shown to be crucial in other studies. For example, the complete anaesthesia of the thumb have been shown to induce a 60-70% increase of its perceived size (Gandevia & Phegan, 1999), while the block of the cutaneous afferents caused a 28% increase of the perceived size of objects held in the hand in the study by Berryman and colleagues (Berryman et al., 2006).

In conclusion, these first two experiments suggest, firstly, that the metric representation of body parts is overall more stable and resistant to the disruption of spatial processing and representation brought about by USN, relatively to non-corporeal objects. Secondly it seems that this advantage for the body may depend upon a visuo-spatial representation of the prototypical shape of the body. Finally, the present work shows that coding the length of body parts and of extrapersonal objects are dissociable functions.

CHAPTER 3

THE BODY AS AN INTRINSIC SYSTEM OF MEASUREMENT

3.1. The body as an intrinsic metric system

Since ancient times humans have adopted metric systems that are based on human body parts (for a description see Nicholson, 1912 cited in (Longo & Lourenco, 2007)). The term “anthropic units” describes a group of measurement units which explicitly arose from human physiology or behaviour. Some of them derived from human activities such as walking or farming, whereas others were derived directly from the standard size of human body segments (i.e., anthropomorphic units), often also taking the name of that specific body part. Fig. 3.1 depicts nine of these historical units of measurement: the yard, the span, the cubit, the Flemish, the English and the French ell, the fathom, the hand, and the foot.

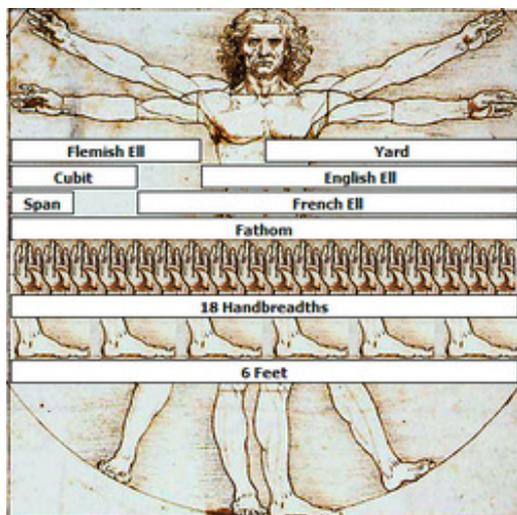


Fig. 3.1

A derivation of the Vitruvian Man by Leonardo da Vinci

The cubit is the first recorded unit of length and was employed through Antiquity, the Middle Ages up to the Early Modern Times, especially for measuring cords and textiles. It was based on the forearm length, namely on the distance from the elbow to the tip of the middle finger;

indeed the Egyptian hieroglyph for the unit shows the symbol of a forearm. Despite the limited usefulness of such a metric system, since body parts length can differ a lot among people, it has to be noted that the use of the body as a system of measurement may have seemed intuitive for some reasons.

Apart from this historical digression, recent evidence have shown that arm length may constitute an intrinsic metric for the representation of near space, suggesting that the distance of objects may be scaled as a proportion of one's arm length (Longo & Lourenco, 2007). In a previous study the authors (Longo & Lourenco, 2006) found a gradual shift in the direction of the attentional bias, on a line bisection task, between near and far space; they then investigated the possibility that arm length relates systematically to the rate at which such a shift occurs. Participants were asked to bisect a line using a laser pointer at eight possible distances ranging from 30 to 240 cm, thus being within and beyond the arm's reaching space. They calculated the size of the near space for each subject by computing the slope of the best-fitting line, regressing rightward bias on distance. They have then hypothesized that if no relation exists between the size of the near space and the arm length, these slopes should be unrelated to the length of participant's arm. On the contrary, if a systematic relation occurs, then an inverse correlation between the arm length and the individual slope should be found. This would lead to the conclusion that people with longer arms show a lower slope indicating a more gradual shift between near and far space, and hence a larger peripersonal space relative to people with shorter arms. Actually, they observed consistent individual differences in the rate at which the shift occurred, indicating a systematic relation to arm length in the direction they have hypothesized [$r(19)=-0.48$; $p<0.05$], suggesting that body parts length, or at least arm length, may functions as an intrinsic metric to define the near space.

In this thesis, Experiment 3 and 4 tested the hypothesis that arm length, and in particular its spatial metric representation, may be implicitly used to scale, and hence better evaluate, the length of a three-dimensional non corporeal object that occupies the same spatial region as the forearm (experiment 3). Furthermore the role of tactile and proprioceptive information for body metrics and space representation was addressed (Experiment 4).

3.2. Experiment 3

In experiment 3 neurologically healthy volunteers performed a bisection task of a cylinder in two different conditions, namely with or without their left forearm placed inside the three-dimensional object. The main hypothesis was that if the metric representation of a body part (i.e., the forearm and the hand in this case) can be used to scale the length of its surrounding space, this should reflect in the spatial representation of non corporeal objects that occupies that same space. Given that experiments 1 and 2 called for a better representation of corporeal than extracorporeal space, here we should expect that participants show better bisection judgements when the forearm and hand are placed inside the cylinder, as compared to the bisection of an empty cylinder at the same spatial location.

3.2.1 Materials and methods

3.2.1.1. Participants

Eighteen right-handed neurologically unimpaired participants (9 females and 9 males; mean age: 24; mean educational level: 15 years) took part in the experiment. All the volunteers gave their informed consent according to the Declaration of Helsinki (BMJ 302 (1991) 1194).

3.2.1.2. Experimental procedure

Participants sat on a chair and were presented with a plastic cylinder placed on a wooden board at a distance of about 20 cm from their body, with the objective midpoint aligned with their midsagittal plane. Participants were required to set the midpoint of the stimulus with their right index finger in two conditions: (a) the left forearm and the left hand were placed inside the cylinder (Fig. 3.2 a); (b) the left elbow was placed at the left end of the cylinder with the left hand touching the left shoulder, so that the amount of proprioceptive information coming from the left side of the stimulus were as equal as possible in both the conditions (Fig. 3.2 b). For each participant a cylinder of a length that perfectly matched his/her forearm plus hand length was built (therefore, eleven different cylinders ranging from 35 cm to 45 cm in length, were used).

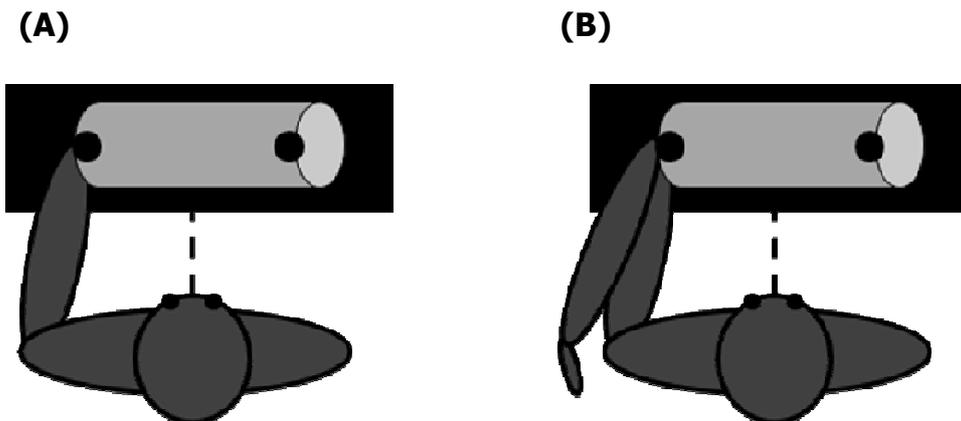


Fig. 3.2
Schematic bird's eye view of the experimental setting.

Participants rested their right index finger touching the body midline and, following a vocal cue given by the experimenter, they were required to point to the midpoint of the cylinder and then put the index finger back to the starting position. The right and left endpoints of the cylinder were clearly indicated to the participant prior to each block of trials. After each pointing, performed with no time constraints and no corrections allowed, the experimenter measured the distance between the left extremity of the stimulus and the point indicated by the participant, at the nearest millimetre.

Participants performed a total of 48 bisections (i.e., 24 for the Cylinder plus Forearm, 24 for the Empty Cylinder) distributed in 4 blocks, each including 12 trials (i.e., two blocks for each condition), following an ABBA design. The block order was counterbalanced between participants. As in Experiment 1 and 2, in order to avoid stereotyped motor responses during the task, in each block a separate line bisection task was interspersed every 4 trials. Participants were asked to set the midpoint of four segments (5 cm long, 1 mm wide), horizontally aligned on an A4 sheet, pointing with their right index finger. A *percentage deviation score* was calculated for each condition by means of the formula used in Experiment 1 and 2. The mean percent deviation scores in each stimulus condition were analyzed by means of a paired t-test.

3.2.2. Results and discussion

Fig. 3.3 shows that participants made overall leftward bisection errors in both the conditions, showing a lower deviation score when their left forearm was placed inside the cylinder (mean deviation score: -2.04% vs. -2.96%, $t(17)=-2.993$; $p<0.01$).

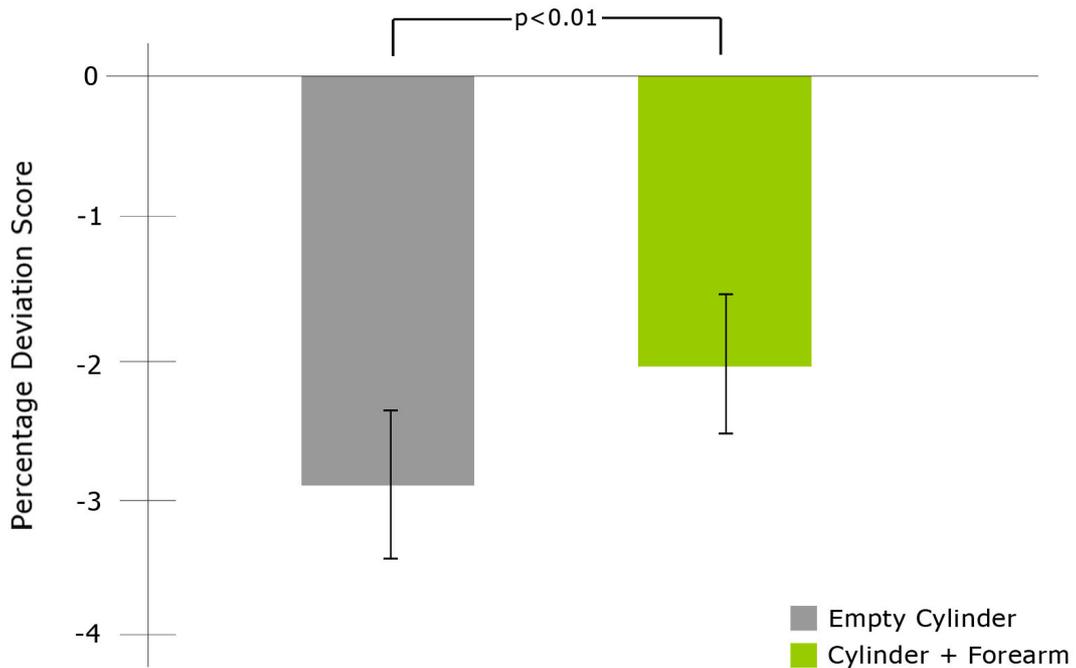


Fig. 3.3 Mean percent deviation score.

Mean percent bisection error (\pm standard errors) in the Empty Cylinder (grey columns) and in the Cylinder plus Forearm (green columns) conditions.

This result suggests that the spatial encoding of an extracorporeal object (i.e., the cylinder) may be facilitated and may become more efficient, thanks to the presence of the forearm in that space, as if in the "Cylinder plus Forearm" condition participants can implicitly rely on a well known metric representation of the forearm to estimate the length of the cylinder. Furthermore, this experiment calls for the importance of proprioception in the automatic coding of the body metrics. Indeed, in the present experiment the presence of the forearm improved the performance even if the forearm was out of visual control.

In this situation, at odds with what discussed for experiment 1 and 2, the influence of the forearm cannot be explained by taking into account the standard and prototypical visual appearance of the body as a reference for spatial analysis (Downing et al., 2001). Rather, one may think that proprioception may be important. Indeed it has been shown a strict relation between the availability of coherent information about body position in space and the stability of the representation of the body as an extended object in space (Longo, Kammers, Gomi, Tsakiris, & Haggard, 2009).

3.3. Proprioception and body representation

Proprioception is the sensory modality by means of which the brain receives information about the position of the body in the external space as well as the relative position of different body parts in respect to each other. Proprioceptive signals are essential to construct the so-called “postural schema”, a concept introduced for the first time by Head and Holmes to indicate a continuously updated representation of the body schema through postural changes (Head & Holmes, 1911). As indicated in a recent review on body representation, “*in order to determine the location of a body part into the external space, information about the configuration of the body (joint angles) must be combined with information about the length of the segments connecting those joints and with information about the width of each body part (p. 658)*” (Longo et al., 2010). Given that any afferent channel is known to carry this kind of information, the authors suggest that knowledge about body size must be stored in a pre-existing body representation. A further specification comes from recent evidence showing that a proprioceptive conflict may induce a modification of body representation. In the well-known Pinocchio illusion (Lackner, 1988) an illusory flexion or extension of the elbow is induced by tendon vibration while participants hold their nose with the hand of the stimulated arm; this produces a perceptual conflict with the hand felt to be moving, towards or away from the body according to the illusory elbow flexion or extension, yet maintaining a continuous contact with the nose. The result is that many participants perceive their nose shrinking or extending, even if, of course, they are perfectly aware that the actual size of their nose was not changing.

Therefore a strict interaction between higher-order cognitive body representation (such as a model containing stable information about body parts' width and length) and the ongoing representation derived constantly updated through proprioception, can be hypothesized. In particular, a recent study (Longo et al., 2009) addressed this issue, capitalizing on the evidence that a vibration applied to arm muscles can change the perceived angle of the forearm flexion or extension (in particular, a vibration applied on the biceps muscle tendon induces an illusion of elbow extension, while a vibration on the triceps tendon induces an illusory flexion). These authors have shown that by inducing a proprioceptive conflict -by means of the simultaneous vibration of antagonistic biceps and triceps muscle tendons- it can be induced an illusory telescoping of the arm towards the elbow. Crucially, when participants received the dual tendon stimulation they were perfectly able to match the position of their right arm with the left one on the vertical axis, but they were significantly biased in a pointing task to body locations (i.e., pointing to the tip of their right index finger or to an elastic ring placed around their right forearm, approximately midway between the elbow and the wrist). Pointing errors were consistently directed towards the elbow across all the blocks of trials, thus *"suggesting that the illusion was a rapid result of absent position information, rather than a progressive drift over time (p. R728)"*. They then replicated the same results in a second experiment using a passive perceptual judgement task. A Plexiglas panel was placed parallel to the right forearm, perpendicularly to the midsagittal plane. The participant's left finger was passively moved along the panel till the participant reported it matched the target position. They observed a clear telescoping effect in the dual tendon vibration condition, while no effect was observed in the control conditions (i.e., "biceps vibration alone" and "dual off tendon vibration"; in the latter condition vibrators were placed on the dorsal and volar aspects of the forearm, distal to elbow, so that they did not produce any illusion of movement). Furthermore, in a third experiment, they investigated if the telescoping effect could reflect a perceived shoulder rotation backwards and thus a perceived backward movement of the whole arm, rather than a change in its perceived size. They asked participants to match with the left arm the position of the right arm during five vibration conditions (i.e., "biceps alone", "triceps alone", "dual tendon", "dual off

tendon”, and “no vibration”). The importance of matching the posture of the entire arm, including the angles of the shoulder, elbow, and wrist was emphasized. In order to directly test whether such illusory movement occurs, they measured the angles of the shoulders while participants made the matching task. They didn’t find any difference in matched joint angles across conditions, thus suggesting that the telescoping effect was not due to an illusory backward movement of the whole arm. These results suggest that a loss of coherent information about body position in space seems to produce a contraction of the body representation, indicating that basic signals about body posture also play an important role in representing the body as an extended object in space. This lead to the question about what happens in brain damaged patients reporting a proprioceptive deficit which is a permanent condition, differently from a reversible experimentally induced condition such as in the study by Longo et al (2009). To this aim Experiment 4 (see paragraph 3.4) analyzed the performance of a group of neurological patients, with or without a deficit in the tactile and proprioceptive sensitivity after a right cerebral lesion, on a bisection task replicating the experimental conditions used in Experiment 3. Thus, Experiment 4 tested whether the availability of a well-working somatosensory-proprioceptive system is necessary to allow the use of the spatial metric representation of body parts as an implicit metric system, useful as example to better evaluate the length of a non corporeal object.

3.4. Experiment 4

As mentioned above in paragraph 3.3, in this experiment the interaction between the somatosensory-proprioceptive system and the spatial metric representation of body parts was investigated. In particular the influence of the intrinsic body metrics information on the evaluation of size estimation of non corporeal objects, in the presence of somatosensory/proprioceptive loss, was investigated. In other words, it was tested if the spatial metric representation of body parts might be distorted, or even not usable, when the somatosensory sensitivity is altered by a cerebral lesion.

3.4.1. Materials and methods

3.4.1.1. Participants

Nine right-handed right-hemisphere-damaged patients (6 males and 3 females; mean age: 71; mean educational level: 8 years) were recruited from the inpatient population of two Neurological Rehabilitation Units (U.O. Riabilitazione Neuromotoria, P.R.M. Bozzolo, A.O. di Mantova, Italia; U.O. Riabilitazione Neuromotoria, Presidio Ospedaliero di Rivolta d'Adda, A.O. di Crema, Italia). Nine right-handed volunteers (6 males and 3 females; mean age: 65; mean educational level: 8 years), with no history or evidence of neurological disease participated in the study as a control group. All participants gave their informed consent according to the Declaration of Helsinki (BMJ 302 (1991) 1194). For the patients' group, inclusion criterion was the presence of a right cerebral lesion with no history or evidence of previous neurological and/or psychiatric disorders. As in Experiment 2 contralesional motor, somatosensory and visual field deficits, including extinction to tactile and/or visual stimuli, were assessed by a standard neurological examination. Anosognosia was also assessed in the motor, somatosensory and visual domain (score range: 0 = unimpaired performance; 3 = maximum deficit; see table 3.1 for details) (Bisiach, Vallar et al., 1986). Also a complete battery evaluating extrapersonal and personal neglect and a test of position sense were administered (performance data are reported in table 3.2.).

| | Age/ gender | Length of illness/ Aetiology | | Lesion site | Neurological examination | | | Anosognosia | | |
|----|----------------|------------------------------------|-----|--|-----------------------------|-----|---|-------------|----|---|
| | | days | | | V | SS | M | V | SS | M |
| P1 | 78/M | 57 | H | Thalamus | + - | + | - | 0 | 0 | 0 |
| P2 | 64/M | 31 | I+H | TPF | + | + | + | 1 | 1 | 1 |
| P3 | 66/M | 76 | I | TPF + insula | + | + | + | 3 | 0 | 0 |
| P4 | 67/F | 50 | I | TPF | ext | + | + | 0 | 0 | 0 |
| P5 | 53/F | 45 | I | Cortical/ subcortical F + insula | - | ext | + | 0 | 0 | 0 |
| P6 | 76/M | 54 | I | Pons | - | - | + | 0 | 0 | 0 |
| P7 | 77/M | 35 | I | Thalamic nuclei | - | - | - | 0 | 0 | 0 |
| P8 | 69/M | 61 | I | Thalamic nuclei | - | - | - | 0 | 0 | 0 |
| P9 | 88/F | 43 | I | Cortical/ subcortical P | - | - | - | 0 | 0 | 0 |

Table 3.1 Demographical and clinical data of the patients

Aetiology: I/H/A=ischaemic/haemorrhagic/aneurysm.

Neurological examination: V/SS/M = visual/somatosensory/motor deficits contralateral to the damaged hemisphere; + = present; - = absent; +- = minor deficit; ext = extinction to double simultaneous stimulation.

3.4.1.2. Neuropsychological battery for extra-personal and personal USN

3.4.1.2.1 Extra-personal USN

(a) Cancellation tasks: Line (Albert, 1973); Letter (Diller & Weinberg, 1977; Vallar et al., 1994);

Star (Wilson et al., 1987).

(b) Bisection of six horizontal lines. See paragraph 2.4.1.2.1 for procedure and scoring.

(c) Drawing tests

(1) Clock drawing. See paragraph 2.4.1.2.1 for procedure and scoring.

(2) Copy of a complex line drawing (Gainotti et al., 1972). See paragraph 2.4.1.2.1 for procedure and scoring

(d) Sentence reading (Pizzamiglio et al., 1992). See paragraph 2.4.1.2.1 for procedure and scoring.

3.4.1.2.2. Personal USN

Patients were asked to reach for the left contralesional elbow, hip, shoulder, knee (or leg), hand and ear, using the right ipsilesional hand (score: 0= unimpaired performance; 3= maximum deficit; score range: 0-18).

3.4.1.2.3. Proprioception

Proprioception was evaluated by means of a modified version of the test used by Vallar and colleagues (Vallar, Antonucci, Guariglia, & Pizzamiglio, 1993). The patient placed the contralesional left forearm under an opaque screen. Four lines were drawn and numbered on the top of the screen, and corresponded to four possible arm positions under the screen. For 20 trials the examiner moved the forearm in one of the four possible position (1: straight-ahead; 2, 3 and 4: 30°, 60° or 90° adduced towards the patient's trunk, respectively). The patient was asked to read the number corresponding to the position in which he/she felt the arm. The test score range is 0-20 (0: maximum deficit; 20: unimpaired performance). Control data were collected from the group of neurologically unimpaired participants who made no errors in this test.

Patients' performances in each test are reported in table 3.2.

| | Line bisection (%) | Line cancellation | | Letter cancellation | | Star cancellation | | Drawing | | Reading | Personal neglect | Proprioception (%) and tactile sensitivity | |
|-----------|--------------------|-------------------|--------|---------------------|--------|-------------------|--------|---------|--------|---------|------------------|--|------|
| | | L | R | L | R | L | R | Copy | Clock | | | P | T |
| P1 | 3.18 | 18/18 | 18/18 | 46/53* | 50/51* | 27/30* | 26/26 | 6/6 | 9.5/10 | 5/5 | 0/18 | 57.5* | 2/3* |
| P2 | 5.6 | 18/18 | 18/18 | 0/53* | 25/51* | 0/30* | 20/26* | 1/6* | 1/10* | 4/5* | 0/18 | 70* | 3/3* |
| P3 | 82.2* | 0/18* | 15/18* | 0/53* | 19/51* | 0/30* | 8/26* | 0/6* | 6/10* | 0/5* | 0/18 | 60* | 3/3* |
| P4 | 4 | 18/18 | 18/18 | 49/53 | 51/51 | 21/30* | 24/26 | 6/6 | 2/10* | 3/5* | 0/18 | 65* | 2/3* |
| P5 | -9.8 | 18/18 | 18/18 | 47/53 | 44/51 | 29/30 | 24/26 | (5/6) | (0/10) | 5/5 | 0/18 | 95* | 1/3* |
| P6 | -1.06 | 18/18 | 18/18 | 50/53 | 50/51 | 28/30 | 26/26 | 6/6 | 8/10 | 5/5 | 0/18 | 100 | 0/3 |
| P7 | -2.40 | 18/18 | 18/18 | 53/53 | 51/51 | 30/30 | 25/26 | (5/6) | 8/10 | 5/5 | 0/18 | 100 | 0/3 |
| P8 | 4.40 | 18/18 | 18/18 | 59/53 | 47/51 | 29/30 | 25/26 | (5/6) | 8/10 | 5/5 | 0/18 | 100 | 0/3 |
| P9 | -5 | 18/18 | 18/18 | 43/53* | 48/51* | 30/30 | 26/26 | (4/6) | 2/10* | 5/5 | 0/18 | 100 | 0/3 |

Tab. 3.2 Neuropsychological baseline assessment for unilateral spatial neglect

Line bisection: percentage of rightward deviation error. Cancellation tests: target detected in the left- and right-hand sides of the sheet (L/R). Drawing, reading, personal neglect and tactile sensitivity (T): patient's score/maximum possible score. Proprioception (P): Percentage of correctly-detected stimuli.

Asterisks indicate a defective score that is due to USN. Brackets indicate a defective score that is not due to USN.

3.4.1.3. Experimental Procedure

The procedure was the same used in Experiment 3 except for the fact that, due to their motor impairment, right-brain damaged patients were unlikely to be able to maintain the left forearm in the position requested in the Empty Cylinder condition. So, in this condition patients put their left hand close to the left extremity of the cylinder. Additionally, in order to maintain the same amount of visual input from both sides, participants wore a black mantle which was fixed to their neck and to the extremities of the cylinder, in order to mask all the visual space around their body and the cylinder. (see Fig. 3.4 a-b).

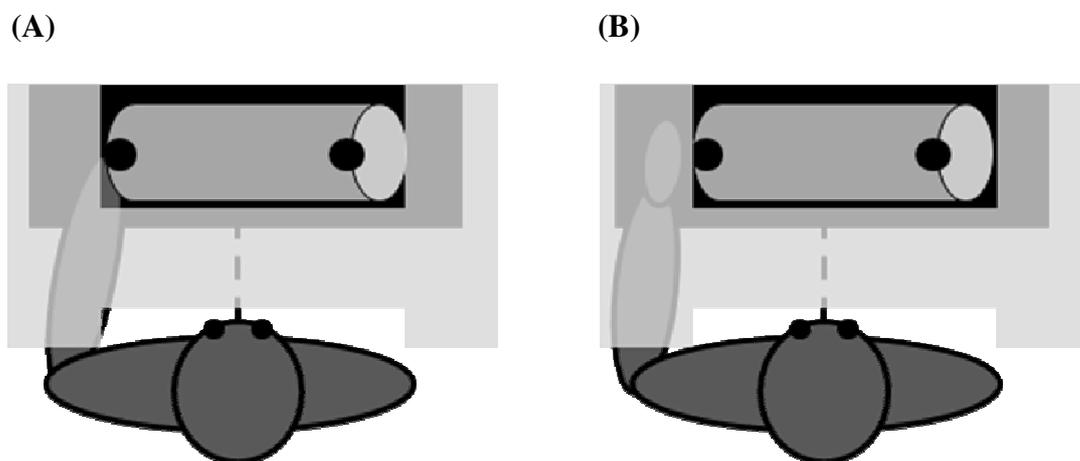


Fig. 3.4
Schematic bird's eye view of the experimental setting.

3.4.2. Results

Five out of eight patients (i.e., patients #1, #2, #3, #4 and #5), reporting a deficit in the somatosensory and proprioceptive sensitivity, were included in the SP+ group, while four patients (i.e., patients #6, #7 #8 and #9) were included in the SP- group since they didn't show any tactile-proprioceptive deficit (see table 3.1 and 3.2 for details).

Fig. 3.5 shows that healthy control participants and patients without any tactile-proprioceptive deficit made overall leftward bisection errors in both conditions, reporting a lower deviation score when their left forearm was placed inside the cylinder. On the contrary, patients in the

SP+ group showed an higher deviation score in the “Cylinder plus Forearm” condition. Furthermore, they made overall rightward bisection errors, consistently with the presence of Unilateral Spatial Neglect in four out of five patients within the SP+ group (note that within the SP- group only one patient showed minor signs of USN, see table 3.2).

A mixed design ANOVA was performed with a within-subjects factor, Stimulus (Empty Cylinder; Cylinder plus Forearm) and a between-subjects factor, Group (Controls; SP+; SP-).

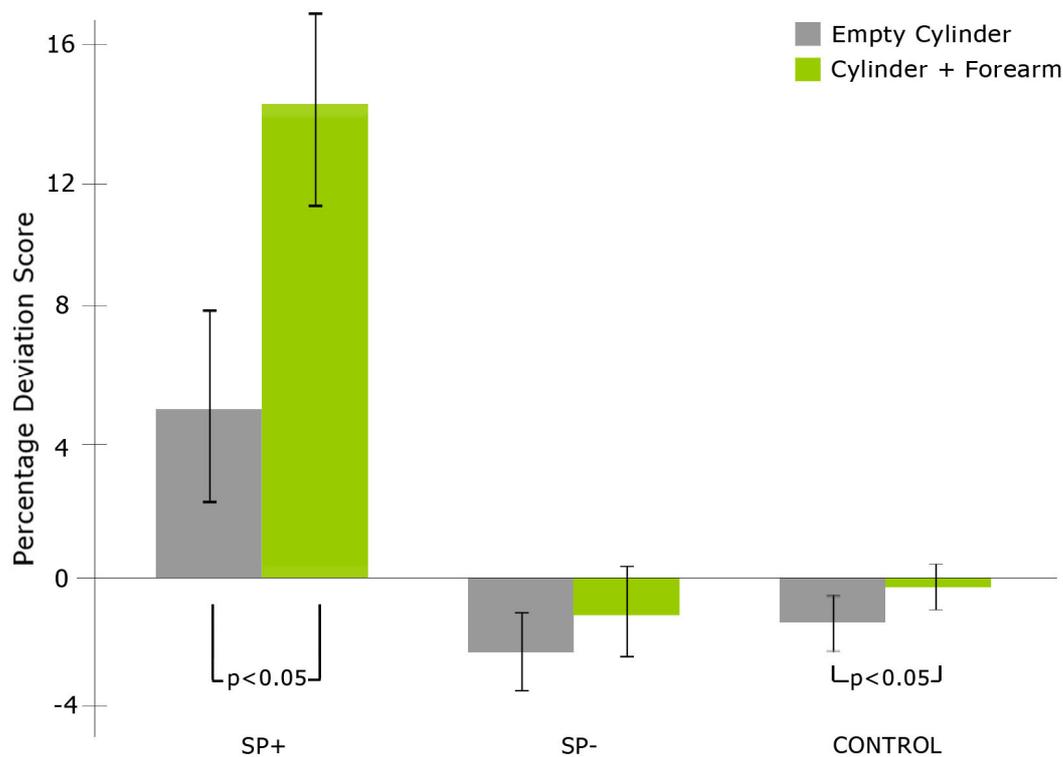


Fig. 3.5 Mean percent deviation score.

Mean percent bisection error (\pm standard errors) in the Empty Cylinder (grey columns) and in the Cylinder plus Forearm (green columns) conditions in the three groups (Controls; SP+ and SP-).

The main factors Group [$F(2,15)=15.15$; $p<0.01$, $\eta^2=0.7$] and Stimulus [$F(1,15)=15.9$; $p<0.01$, $\eta^2=0.34$] and the interaction Group by Stimulus [$F(2,15)=8.2$; $p<0.01$, $\eta^2=0.35$] reached the significant level. Bonferroni Post Hoc multiple comparisons showed a significant difference between the performance of the SP+ group relative to the SP- and control groups, while no difference emerged between the SP- group and the control participants (SP+ vs.

Control: $p < 0.01$; SP+ vs. SP-: $p < 0.01$]. A further analysis of the interaction Group by Stimulus, performed by means of paired t-tests, revealed that the difference between the two bisection conditions was significant only in the SP+ and in the control groups (SP+: mean deviation score: 4.76% vs. 14.33%; $p < 0.05$; Controls: mean deviation score: -1.64% vs. -0.39%; $p < 0.05$), whereas only a trend to a significant difference was found in the SP- group (mean deviation score: -2.55% vs. -1.58%; $p = 0.095$). This latter result may well be due to the small size of the sample (i.e., $n = 4$). Despite this latter comparison didn't reach the significance, a clear trend with SP- patients performing better in the Cylinder plus Forearm condition than in the Empty Cylinder one, similarly to the control group.

On the contrary, SP+ patients showed the opposite pattern, displaying a less accurate performance when their left forearm was placed inside the cylinder. Furthermore, by means of the Revised Standardized Difference Test (Crawford & Garthwaite, 2005), the difference between the two bisection conditions in each patient was compared with the same difference in the control group (see Fig. 3.6).

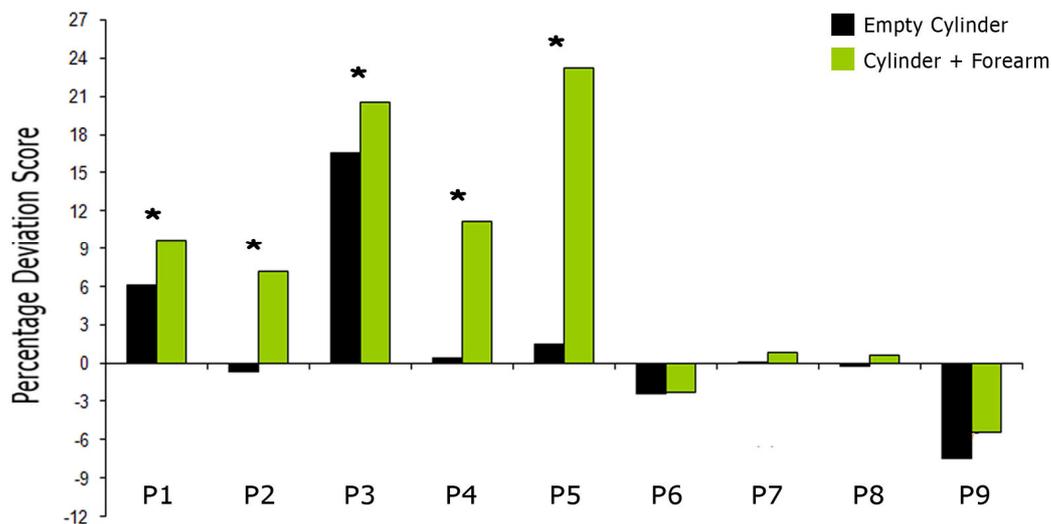


Fig. 3.6 Mean percent deviation score by stimulus condition in the P+ and P- groups.

Asterisks indicate a significance difference between the two bisection conditions in the individual patient, as compared to the same average difference in the control group.

All the patients within the SP+ group showed a significant difference relative to the healthy participants (patient #1: -3.55%, $t(8)=2.369$; $p<0.05$; patient #2: -7.83%, $t(8)=4.499$; $p<0.01$; patient #3: -3.95%, $t(8)=3.512$; $p<0.01$; patient #4: -10.83%, $t(8)=6.144$; $p<0.01$; patient #5: -21.69%, $t(8)=10.482$; $p<0.01$), while any patients in the SP- group showed a difference relative to the control group, thus confirming that their performance can be considered in line with healthy participants' one (patient #6: -0.18%, $t(8)=0.865$; $p= n.s.$; patient #7: -0.83%, $t(8)=0.151$; $p= n.s.$; patient #8: -0.77%, $t(8)=0.211$; $p=n.s.$; patient #9: -2.09%, $t(8)=0.057$; $p= n.s.$).

3.5. Discussion

In the experiments reported in the present chapter, a critical experimental question was investigated, namely whether the spatial metric representation of the body may implicitly influence the spatial coding of extrapersonal objects that share a common space with the body and whether a similar effect is based on the availability of efficient tactile and proprioceptive information. In particular, Experiment 3 demonstrates that the visuo-spatial analysis of an object's length can be facilitated by the presence of a body part into the space occupied by the object. This result is in line with the findings by Longo and Lourenco (Longo & Lourenco, 2007), suggesting that body parts length can be used as an intrinsic metric parameter in order to determine the boundaries between near and far space, and thus defining the extension of the peripersonal space. The present results extend this previous result, by suggesting that the presence of a body part active scales the metric judgement relative to objects in its surrounding space in an online, continuous fashion. In this respect, a recent review (Longo et al., 2010) highlights the importance of a pre-existing representation of the body in order to allow what the authors name called "somatoperception", that is a class of processes comprising the ability to localize tactile stimuli on the skin surface, perceive the metric properties – such as length, size, width and shape- of objects touching the skin, perceive the location of body parts in the external space as well as the location of objects touching the body in the external space. In the critical condition "Cylinder plus Forearm" of Experiment 3 the skin surface placed into the

cylinder, and thus touching the board, exactly matched the length of the cylinder itself, providing a further afferent somatosensory information that could have been used in order to better evaluate the length of the object, and hence to better perform the bisection task. As hypothesized by Longo et al. (2010) indeed *"we can perceive the size of objects touching a single skin surface on the basis of the extent of skin surface touched"*, but in order to allow the estimation of the object size this afferent information must be referred to a pre-existing representation of the body size. Indeed, primary somatosensory maps are thought to be distorted by various factors, such as the density and receptive fields of mechanoreceptors in the skin, the receptive field size of the cortical units and the over-representation of certain skin region, such as fingers and lips in cortical sensory maps. Furthermore, it has been reported that the magnitude of Weber's illusion⁴ should be significantly higher on the basis of tactile acuity or cortical magnification, suggesting that -in order to provide an approximately veridical perception of tactile size- a sort of "tactile size constancy" should correct for distortions produced in the primary representations. A model of the actual metric properties of the body seems to be necessary to allow this sort of correction (Taylor-Clarke et al., 2004). The strict relation between somatosensory input and higher-order metric representation of the body is additionally highlighted by the fact that, although there are no peripheral receptors informing the brain about body parts size, alterations of perceived body size were reported after peripheral deafferentation. Recent evidence showed that the perceived size of objects held between the fingertips was increased by 28% when cutaneous input were blocked by anaesthesia (Berryman et al., 2006); additionally participants reported their fingers to be swollen when they were under anaesthesia. With this respect, Gandevia and Phegan (Gandevia & Phegan, 1999) demonstrated that after a complete anaesthesia of the thumb -by means of a digital nerve block- its perceived length and width were significantly increased by 60-70%, while no changes occurred to the perceived size of the adjacent fingers. Furthermore in a more recent study it was shown, in 36 patients undergoing orthopaedic surgery, that perceptual changes about the

⁴ Illusory perception of an increasing distance between two points on the skin when the points are moved from a lower to a higher sensitivity region.

shape and size of a deafferented limb (i.e, the forearm or the leg) occurred always in association with the impairment of thermal and pinprick sensations. Thus, the authors suggested that the small myelinated A δ - and/or the unmyelinated C-fibres may provide a source of important information to the limb's cortical representation (Paqueron et al., 2003). In this respect, the results of Experiment 3 point to the role of a multisensory construction of the metric qualities of body representation that is not only derived by vision (as it was suggested by experiment 2) but also constructed through somatosensory input. Experiment 4 further support this view by showing that when right-brain damaged patients with tactile and proprioceptive defects are asked to spatially analyze a three dimensional object, they not only cannot take advantage of the presence of their left arm inside the object, but they also show a disadvantage in this condition, relative to the control condition. A possible interpretation could be that in the lack of somatosensory information regarding the forearm, its metric representation is less defined, possibly even enlarged, mimicking the case of somatosensory deafferentation as reported above (Berryman et al., 2006; Gandevia & Phegan, 1999). If this was the case, then participants -having a distorted longer representation of the arm- will set the midpoint of the cylinder more rightwards in the Cylinder plus Forearm condition, than in the Empty Cylinder condition, as found in Experiment 4. This would lead to the conclusion that the spatial metric representation of body parts might be altered by the loss of sensory information referred to that body part. This is only an hypothetical interpretation, because it cannot actually be excluded that the differences between the two groups of patients (i.e., SP+ and SP-) are merely due to the site and the extent of the lesion (actually much larger in the SP+ than in the SP- group), or to the fact that in the SP+ group, besides the somatosensory-proprioceptive deficit, also the spatial metric representation of body parts is distorted per se. Nevertheless, it has to be noted that the results reported here further support the hypothesis that a spatial metric representation of body parts exists, and it can be used to scale the size of extrapersonal objects in the external space. This metric representation can be critically altered by cerebral lesions even if it's not yet clear whether the distortion regards the metric representation itself or the afferent input necessary to build up such a representation.

Furthermore the present experiment suggests that the influence of body parts on the metric scaling of it's surrounding space would be almost entirely unconscious, since, in the Cylinder plus Forearm condition, participants were asked to perform the task referring to the cylinder, as in the control condition, and without emphasizing the fact that the arm was placed inside the cylinder and thus without focussing the attention of the subject on the forearm.

CHAPTER 4

DYNAMIC CHANGES IN THE METRICS OF BODY PARTS

INDUCED BY TOOL-USE

4.1. Tool use modifies the extent of the reaching space

The use of tools has represented a fundamental evolutionary stage within the human species development. Even non-human primates can, more or less spontaneously, utilize functional tools, but the degree of accuracy and the multiplicity of aims that human tool-use has reached is by far superior to any other primate. Tools can be used to various aims, but they often serve the scope of extending the possibility to act in the space beyond hand's reach, as if our hands were elongated to reach a previously unreachable position. The result is an extension of the so called peripersonal space, which is alternatively definable as the "space of action". Early evidence in this field of research came from neurophysiological studies on the macaque brain. Iriki and coworkers (Iriki et al., 1996) registered the firing activity of "bimodal neurons" located in the intraparietal cortex of the monkeys' brain. These bimodal neurones respond to somatosensory stimuli presented on the hand of the monkey and to visual stimuli presented into the space immediately surrounding the hand. The monkey was instructed to use a rake to retrieve pieces of apple placed beyond hand's reach, but reachable with the rake, for about 15 minutes. After this training phase some of the bimodal neurons recorded expanded their visual receptive field to include the entire length of the rake; thus, after tool use, these neurones were activated by visual stimuli presented at the tip of the tool as well as by visual stimuli presented at the hand. Interestingly, no change in their visual receptive field was found after a five-minute passive holding of the rake, suggesting that active use of the tool is a critical requirement to generate a recoding of the far space as near space. The expansion of receptive field was supposed to be a possible neural substrate of use-dependent assimilation of the tool into the body schema. Additionally, the bimodal neurons involved in this process were those

parietal neurons with a tactile receptive field located on the arm/hand and not those with a somatosensory receptive field centred on the fingers; this was specificity supposed to reflect the fact that the rake, allowing a farther reaching, but not a precise grasping, actually represents an extension of the forearm and the hand, but not of the fingers.

The effect of tool use has been then investigated in humans, both in behavioural studies on healthy participants (Maravita, Spence et al., 2002) and in neuropsychological studies on neglect and extinction patients (Berti & Frassinetti, 2000; Farnè et al., 2005; Farnè & Làdavas, 2000; Maravita et al., 2001). To this aim Maravita and colleagues (Maravita, Spence et al., 2002) used the cross-modal visuo-tactile interference effect⁵, which is known to produce a stronger interference of visual distractors on the detection of tactile targets when presented close to the tactile target, relative to the condition in which the distractors are located far away, on the opposite hemifield (Charles Spence, Pavani, Maravita, & Holmes, 2004). More importantly to this study is the evidence that this "side effect" reverses if participants cross the hands (i.e., in this condition the visual distractors on the right side become more effective in inducing the interference effect on tactile stimuli presented at the left hand and vice versa). Interestingly, Maravita and colleagues (2002) found a similar reversal of the "side effect" when participants crossed the tips of two rakes without crossing their hands; thus, when the tip of each tool reached the visual distractors located in the contralateral side of space -relative to the tactually stimulated hand- these distractors induced a stronger interference effect than the ipsilateral ones, even if the posture of the hands remained unchanged. Intriguingly, the reversal occurred if participants actively switched the position of the tools, but not in the case they were passively moved by the experimenter. These data were interpreted as evidence that the rakes have been included into the body schema, as an extension of the real hands along the space

⁵ Rapid localization judgements of tactile stimuli on the fingertips can be substantially interfered by visual distractors (i.e., two LED flashes) presented close to the same fingertips, but in a spatially incongruent position on the vertical axis (e.g., in the typical setting participants hold a cube in each hand with the index above and the thumb below; two small LEDs are placed in the same positions on each cube). Detection of a slight touch under the index fingertip (above position) can be delayed or even disrupted by a small flash presented close to the thumb (below position) and vice versa.

occupied by the tool. Further clues came from neuropsychological studies with right-brain damaged patients exhibiting neglect and/or extinction of contralesional stimuli. Berti and Frassinetti examined the effect of tool-use in patient P.P. who showed a selective neglect for the peripersonal space (Berti & Frassinetti, 2000). When asked to perform a standard pencil-and-paper bisection task, P.P. typically displaced rightwards the midpoint of the line. By contrast, her performance was flawless when she used a laser pointer to bisect a line located in the far space (at a distance of approximately 1 m). Interestingly, her performance was again pathological when she was asked to use a long stick, with which she physically reached the line. The authors suggested that reaching of the far space by means of a tool determined the recoding of that space as near space; since the representation of the peripersonal space was specifically affected by the brain lesion, neglect extended to the far space when the tool use has caused its remapping as near space. Similarly, Farnè and colleagues (2000) showed, in a group of patients exhibiting cross-modal extinction, the possibility that the peripersonal space is extended by tool use. They measured the rate of cross-modal extinction of a tactile stimulus on the contralesional hand by a visual distractor (di Pellegrino et al., 1997) placed at the tip of a 38 cm-long rake kept in the patient's ipsilesional hand. After a training with the rake, in which they were asked to retrieve objects in the far space for 5 minutes, the rate of cross-modal extinction increased relative to the rate measured before tool use. The authors suggested that this finding can be considered as evidence that the peri-hand space extended along the tool axis thus increasing the effect of the ipsilesional visual stimulus at the tip of the tool in inducing extinction of the contralesional touch.

In a further single-case study, it was additionally shown that, in order to induce the putative remapping of the far space as near space, a physical connection between the tool and the patient's hand is required (Maravita et al., 2001). In this study patient B.V. showed an higher cross-modal extinction of tactile stimuli on the left hand when visual stimuli were presented in the near, but not in the far, space. However, if the patient held a stick, with which he could reach the visual stimuli, the visuo-tactile extinction rate in the far space increased. Interestingly, this effect did not occur if the stick laid passively on the table, leaving a gap between the tool

and the patient's hand, thus suggesting that the mechanism underlying the phenomenon of cross-modal extinction depends on the presence of the two stimuli (i.e., visual and tactile) within the same "action space" and, hence, that holding a tool with a hand induces the extension of its "action space" along the tool axis, beyond the hand reach.

Farnè and co-workers (2005) added further evidence to this field of research specifying, firstly, that the remapping does not occur in case of passive use by the participants (see Maravita et al., 2002 for related results in healthy subjects) and, secondly, that the peri-hand space extension is directly related to the functional length of the tool. In particular, patients showed a higher amount of cross-modal extinction by visual stimuli presented close to the hand, than in the far space; interestingly, the rate of extinction did not change after 5 minutes of passive exposure to a 60 cm-long rake, during which patients must only passively hold the tool⁶. Thus, the authors concluded that in order to obtain an inclusion of the tool into the multisensory peripersonal space, an active use of the tool is required. They then investigated the role of the functional length of the tool comparing the extinction rate in the far space (at a 60 cm distance) after the use of a 60 cm-long regular tool, a 30 cm-long regular tool and a modified rake which, despite having a length of 60 cm, had its functional part at 30 cm away from the hand. They observed a less severe amount of visuo-tactile extinction with the modified rake than with the standard 60 cm-long tool, while comparable effects were induced by the use of a regular 30 cm-long tool and the modified rake, thus indicating that what is crucial is not the absolute length of the tool, but the distance at which its operative part is located.

Two more recent studies (Bonifazi et al., 2007; Farnè et al., 2007) give support to the idea that tool use really extends the peri-hand space to include the whole length of the tool. They measured the degree of visuo-tactile extinction at three different locations (i.e., at the handle, at the tip and at the midpoint between the two extremities of the tool). This experiment found

⁶ At a first glance this result seems in contrast with the data previously reported (Maravita et al., 2001), but it should be noted that in the task administered by Maravita and colleagues the patient was instructed to control the orientation of the stick in order to point its tip on a 50-cm distant mark. Thus, if one consider this task as an active use of the tool, then the inconsistency between the two studies is only apparent.

an increased severity after tool use both at the tool-tip and at the middle-tool location, while – according to the hypothesis- no effect was found at the handle of the tool. These results did not support the alternative hypothesis of a mere shift of the visuo-tactile attention to the tool-tip (Holmes, Calvert, & Spence, 2004), whereas clearly favour the main hypothesis of a whole embodiment of the entire tool into the peripersonal space representation.

4.2. Does tool use modify the mental body representation?

The rich body of evidence presented above suggest that the peripersonal space is a multisensory integrative representation characterized by dynamic properties. In particular, using paradigms of tool-use in animals and in human participants (either healthy controls or neuropsychological patients), several authors demonstrated that such a multisensory visuo-tactile space can be extended beyond the space immediately reaching by the hand in a sort of enlarged peripersonal space representation. The consequence of this dynamic process would be to create an area at the tool-tip, where the aimed action actually occurs, that acquires the same multisensory properties that are typical of the near peripersonal space, thus allowing efficient interactions with objects placed in that space. All the studies reported in paragraph 4.1. suggested that the dynamic changes observed in the multisensory properties of peripersonal space after tool use may reflect changes occurring at the level of the body schema. However, as noticed in a recent review on this issue, even if it's plausible to hypothesize that a change in the body schema may be critical to exert a better control on the tool and thus efficiently act in the far space, so far few studies tried to directly test if the observed effects can be ascribed to a quantitative change into the body representation and/or in the peripersonal space representation (Cardinali, Brozzoli et al., 2009). They suggested the analysis of the kinematics of bodily movement as a sensitive test of the body schema properties and its plastic modifications. In a subsequent paper by the same research group, a morphological updating of the body schema induced by tool-use was indeed demonstrated (Cardinali, Frassinetti et al., 2009). In this study participants were trained to use a 40 cm-long mechanical grabber to reach and grasp a target object. Free-hand grasping actions were recorded before and after the tool

use, showing a change in their kinematics parameters (i.e. a reduction of the peak velocity of the transport component of the movement), as if the subjects were indeed performing the movement with a longer arm following tool-use. Furthermore these changes were selective for the transport phase of the movement and, since the grasping phase was not altered, they were also independent from the size of the object. Additionally, untrained movements with a transport component, such as pointing, were similarly affected by the tool-use effect. The selectivity of the tool-use effect on the transport phase of free-hand movements, and its generalization to other actions sharing this component, clearly favour the hypothesis of a modification of the underlying body representation. Again, asking blindfolded participants to point towards the location of a perceived tactile stimulus alternatively delivered to the elbow, the wrist and the middle fingertip, they found an increased perceived distance between the elbow and the middle fingertip after tool use. This latter finding was interpreted as the consequence of a change in the somatosensory representation of the body which is consistent with an increase of the perceived-represented arm length. In this framework, the experimental question of the next experiment, described in paragraph 4.3, was to investigate to what extent tool-use may alter the representation of body metrics. We therefore trained neurologically unimpaired participants to use a long rake to operate in far space, measuring the consequences of tool-use in a direct behavioural task, explicitly requiring the referral to a metric representation of body parts.

4.3. Experiment 5

Experiment 5 investigated the possibility that the spatial metric representation of body parts holds dynamic plastic properties. In particular –and differently from the most part of the studies reported in literature, which have actually investigated the plastic properties of the peripersonal space- in the present experiment, the hypothesis of a dynamic change in the internal representation of body parts length, due to tool use, was directly tested through a behavioural measurement of its metric properties before and after tool use.

4.3.1 Materials and methods

4.3.1.1. Participants

Eleven right-handed volunteers (8 females and 3 males; mean age: 29; mean educational level: 18 years) participated in the study. All the volunteers gave their informed consent according to the Declaration of Helsinki (BMJ 302 (1991) 1194).

4.3.1.2. Experimental procedure

Participants were asked to perform a radial bisection of their right arm before and after a motor training with a tool. They sat blindfolded on a chair with their right forearm placed on a plain surface on the right side. A transparent screen was placed above the arm in order to avoid tactile feedback during the task, which could have influenced the performance. The vertical distance between the screen and the arm was maintained stable between subjects (see Fig. 4.1 a). The experimenter gave a vocal cue at the beginning of each trial and participants were instructed to indicate the radial midpoint of their forearm (considered from the elbow to the tip of the middle finger) using their left index finger.

There was no time constraint, but corrections were not allowed. A paper rule was placed on the top of the plastic screen, with the 0cm point exactly above the tip of the middle finger. This facilitated the experimenter to register the point (p) indicated by the participant. Afterwards a percentage score was calculated by means of the following formula:

$$[(p/arm\ length)*100]$$

A value higher than 50% indicated a deviation of the subjective midpoint towards the elbow, while a value lower than 50% indicated a deviation towards the hand. Participants performed a total of 30 trials (15 before and 15 after the training). At the end of the experiment they were asked to judge, on a 0-10 scale (0: no pain/numbness at all; 10: the strongest imaginable pain), the level of pain/numbness eventually caused by the use of the tool during the training, in order to assess whether any effect of tool-use on body perception could be related to general fatigue effects.

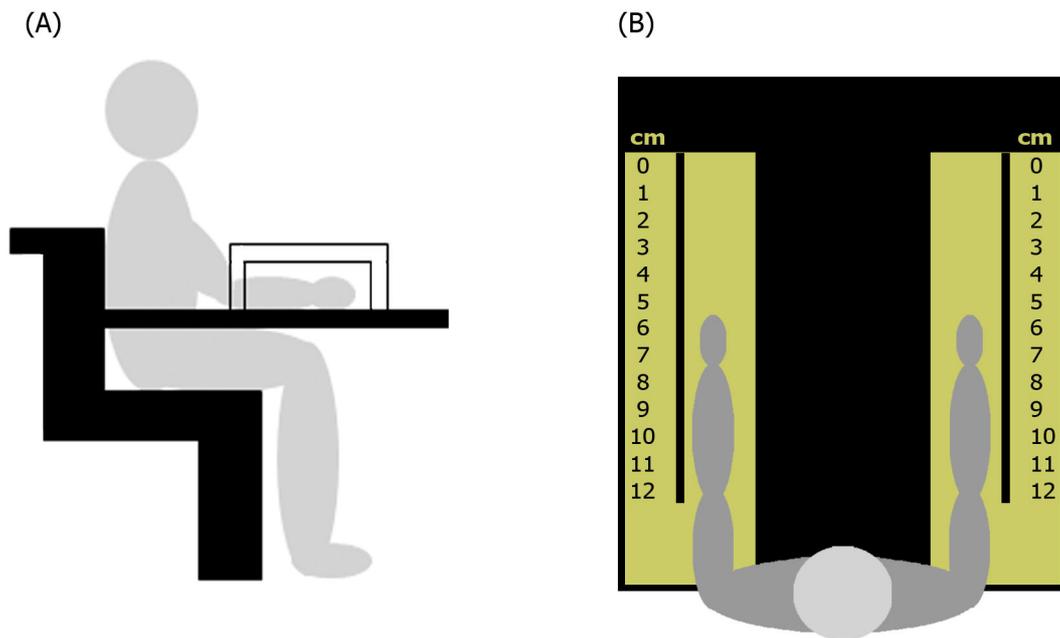


Fig. 4.1 Experimental setting

Schematic view of the experimental setting during the radial bisection of the forearm (a) performed in Experiment 5 and 6 and during the proprioceptive matching task (b) performed only in Experiment 6.

4.3.1.3. Training

A tool consisting of a 60 cm-long stick was used. A nail was fixed at the distal extremity and the participant was instructed to pick up or move fifteen 7 X 3.5 X 2 cm parallelepiped-targets made with polystyrene. Each target displayed a coloured number on its four principal faces. Participants wielded the stick with their right dominant hand. The training, consisting of 4 different tasks, lasted about 15 minutes. They were required to be as much accurate as possible. No participant reported pain after the training; they only reported a slight numbness. Their overall judgement, on a scale from 0 to 10, was 1.18 (\pm 0.9 s.d.) in Experiment 5; while in Experiment 6 it was 1.7 (\pm 1.6 s.d.) and 1.4 (\pm 1.3 s.d.), respectively for the dominant and the non-dominant arm. No significant difference emerged between the degree of numbness reported for the dominant and the non-dominant arm [$t(11)=0.54$; $p=n.s.$].

- *Task 1*

The targets were placed at a distance of about 140 cm from the participant's body, with the coloured number clearly visible (Fig. 4.2).

The experimenter named a colour and the participant was instructed to pick one of the targets displaying a number written in that colour. In order to pick it up participants had to hit with the nail the centre of a cross drawn on the upper face of the target. Once they got the target they had to bring it close to the body, pick it up with the left hand and place it in the spatial position displaying the same number (see Fig. 4.2.). They were instructed to make a continuous, fluid movement and to rest the arm back on the arm-rest on the right side at the end of each trial.

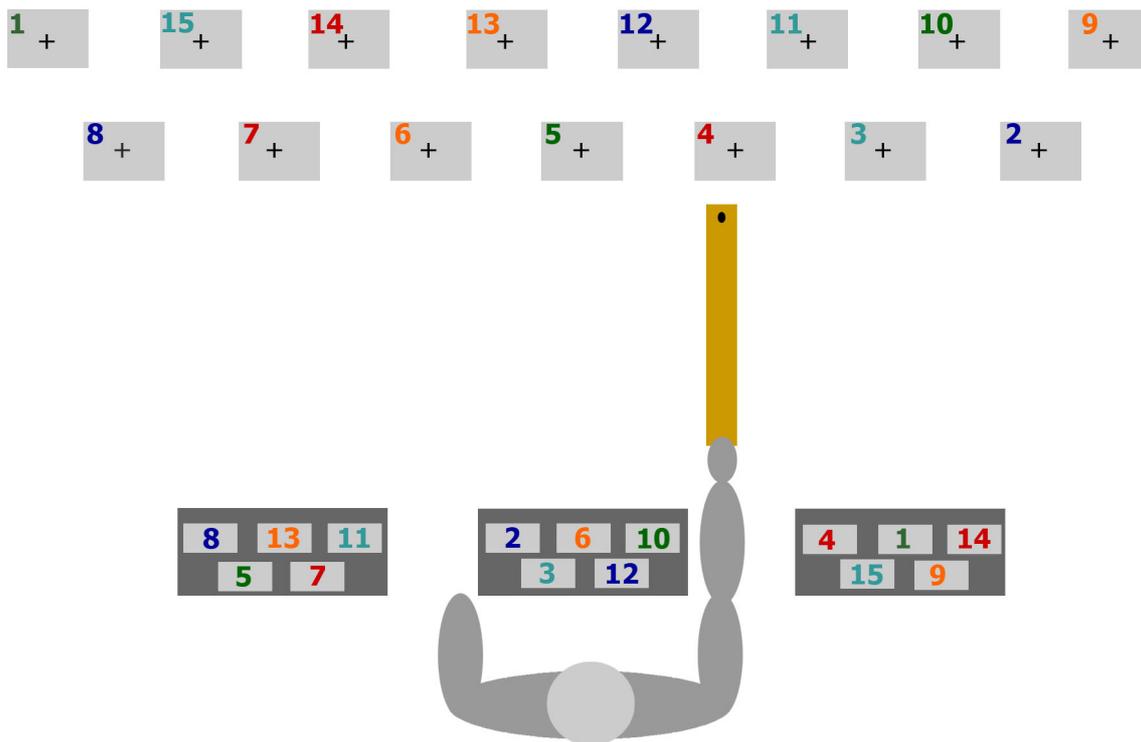


Fig. 4.2 Task 1

Schematic bird's eye view of task 1.

- *Task 2*

After placing the targets back at the starting position, participants were now instructed to pick up the target displaying the number named by the experimenter, hitting the centre of the cross drawn on its upper face. Then, they had to take it again with the left hand and sort it in the correspondent box, depending on the fact that the number was even or odd (see Fig. 4.3.). Once again they were instructed to make a natural and fluid movement and to rest the arm on the arm-rest on the right side at the end of each trial.

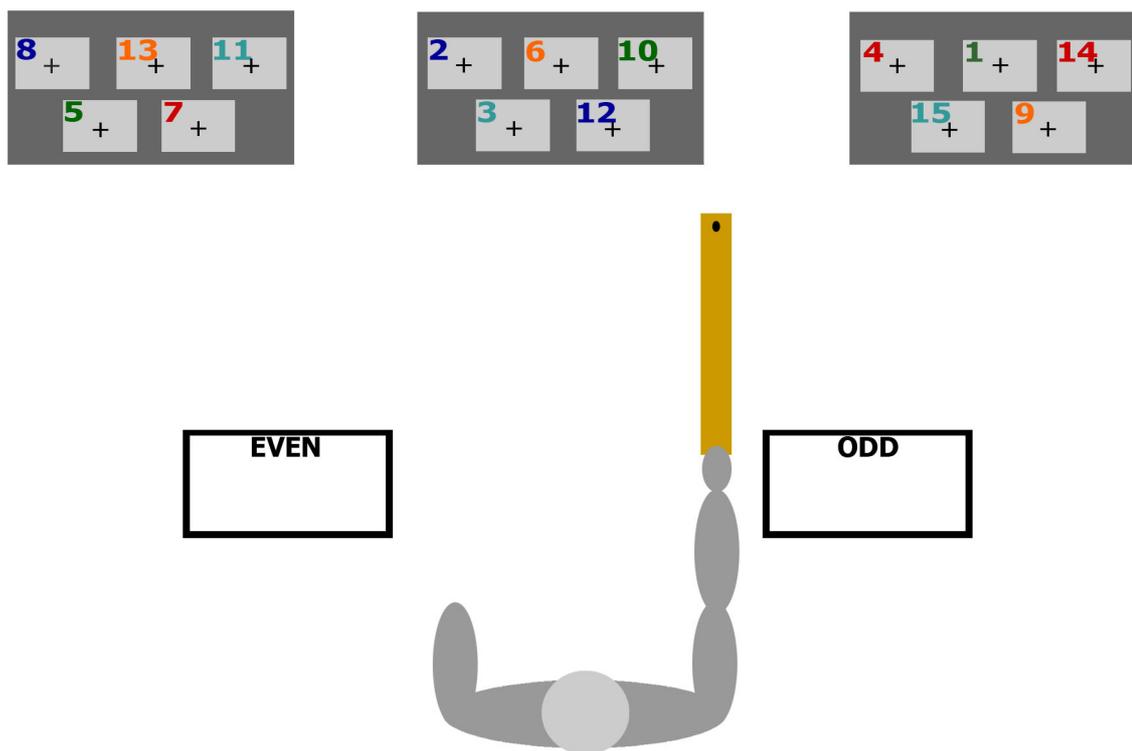


Fig. 4.3 Task 2

Schematic bird's view of task 2.

In task 3 and 4 the stick was used as a rake in order to move the targets consistently with task instructions. In order to make the rod usable as a rake a 15 X 10 X 1 cm piece of plastic material was fixed on the distal nail.

- *Task 3*

The targets were placed close to the participant's body in a random order. Participants had to move the pieces, starting from number 1, to a template displaying the numbers from 1 to 15 as in a domino scheme (see Fig. 4.4). There were no time constraints, but participants were required to be as accurate as possible.

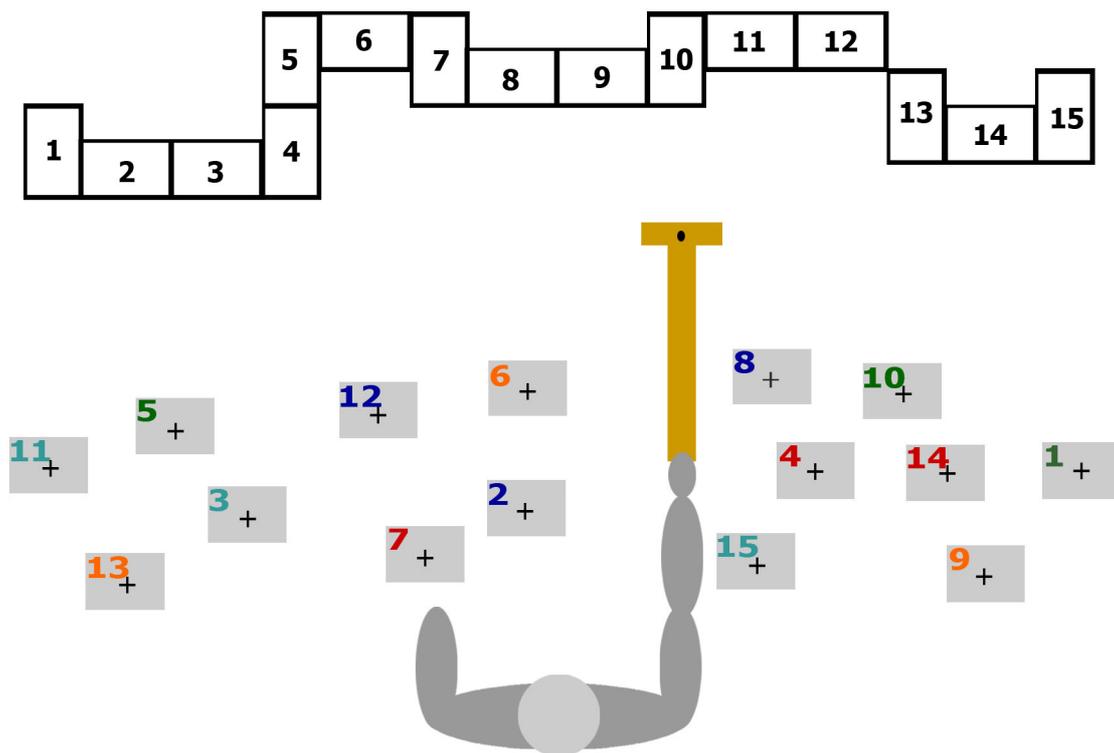


Fig. 4.4 Task 3
Schematic bird's view of task 3.

- *Task 4*

During this task participants were blindfolded. The experimenter scattered the targets all over the table and participants were asked to explore with the tool the space in front of them, trying to retrieve the targets and move them close to their body midline (see Fig. 4.5). At the end of this last task participants were instructed to place their right arm on the arm-rest on their right side in order to perform the post-training bisection task.

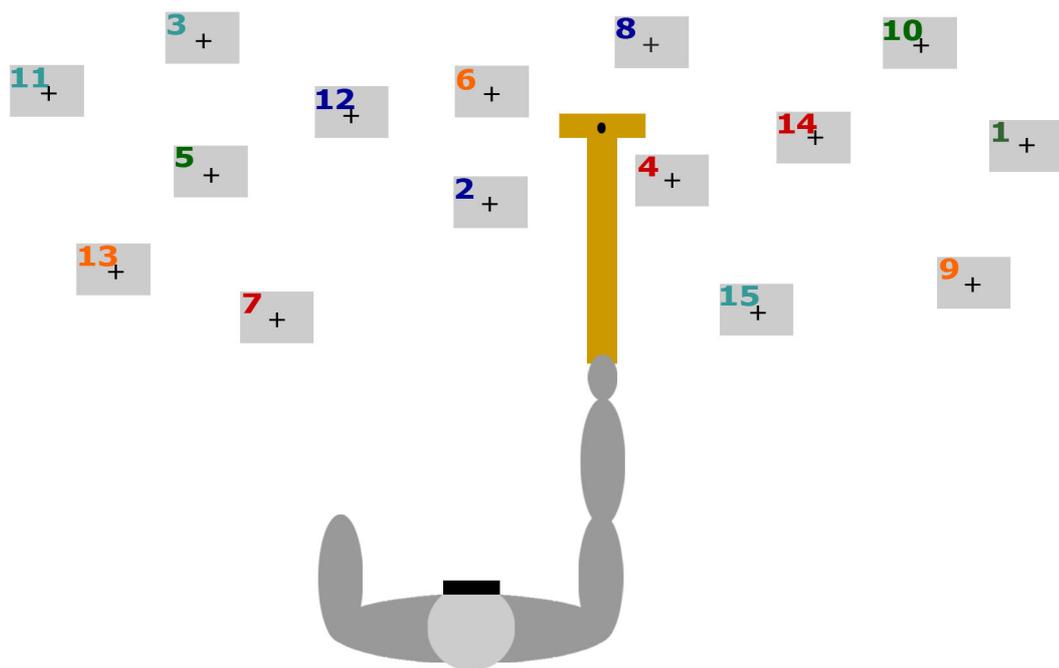


Fig. 4.5 Task 4

Schematic bird's view of task 4.

4.3.2. Results and discussion

The results of the bisection task performed before and after the training is shown in Figure 4.6. As predicted, after the training participants tend to indicate the subjective midpoint of their arm more distally relative to the pre-training measurement (44.92% vs. 48.73%). A paired t-test revealed that this difference was statistically significant [$t(10)=3.309$; $p<0.01$].

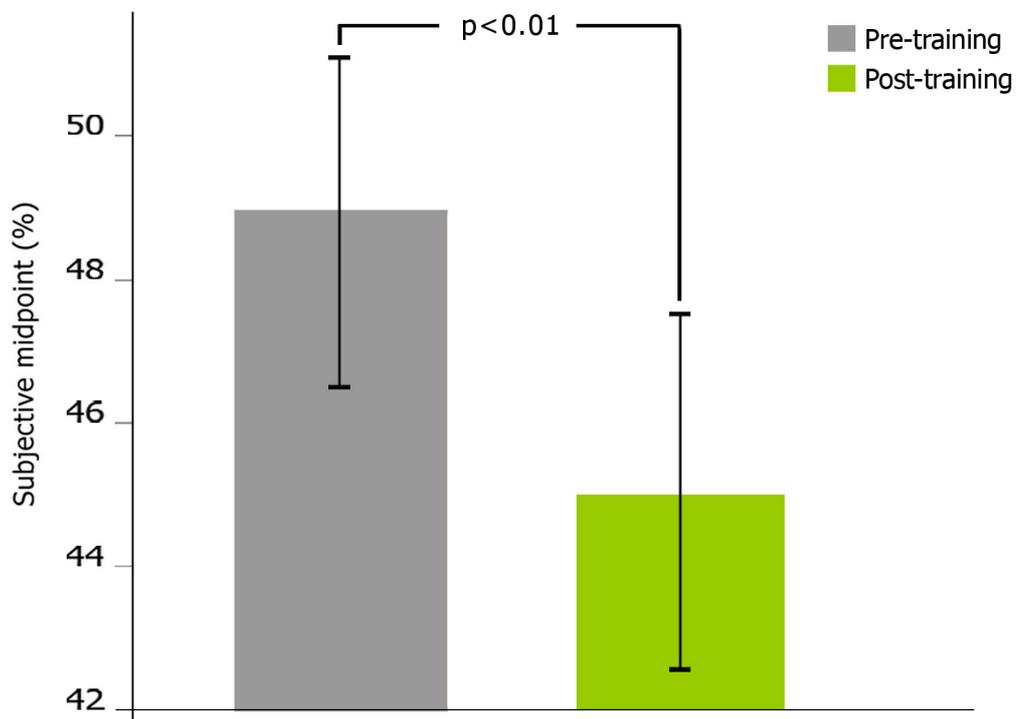


Fig. 4.6 Mean subjective midpoint (%)

Mean percent subjective midpoint (\pm standard errors) before and after the use of a 60 cm-long tool.

This result is in line with the hypothesis of an extension of the metric representation of body parts, as if the arm had been lengthened, as a consequence of tool use. Actually the tool allowed participants to reach the far space, thus extending the reachable space by 60 centimeters. It is possible that such an extension of action space produced a change in the representation of the arm length. A possible opposite interpretation may be that the mere fact to act in the surrounding space, reaching for objects placed in the space in front of the

participant, causes the tendency to bisect the arm more distally after the training, as if, an attentional reweighting of the distal part of the arm occurs after its prolonged use during the training phase. Against this explanation it has to be noted that in a control study replicating exactly the same setting and experimental procedure, except for the tool length (i.e., 20 cm instead of 60 cm) and of course the distance at which the objects were placed during the training, no difference was found between the pre and post training arm bisection task (45.07% vs. 49.02%; $t(10)=-1.66$; $p=n.s.$; see Fig. 4.7).

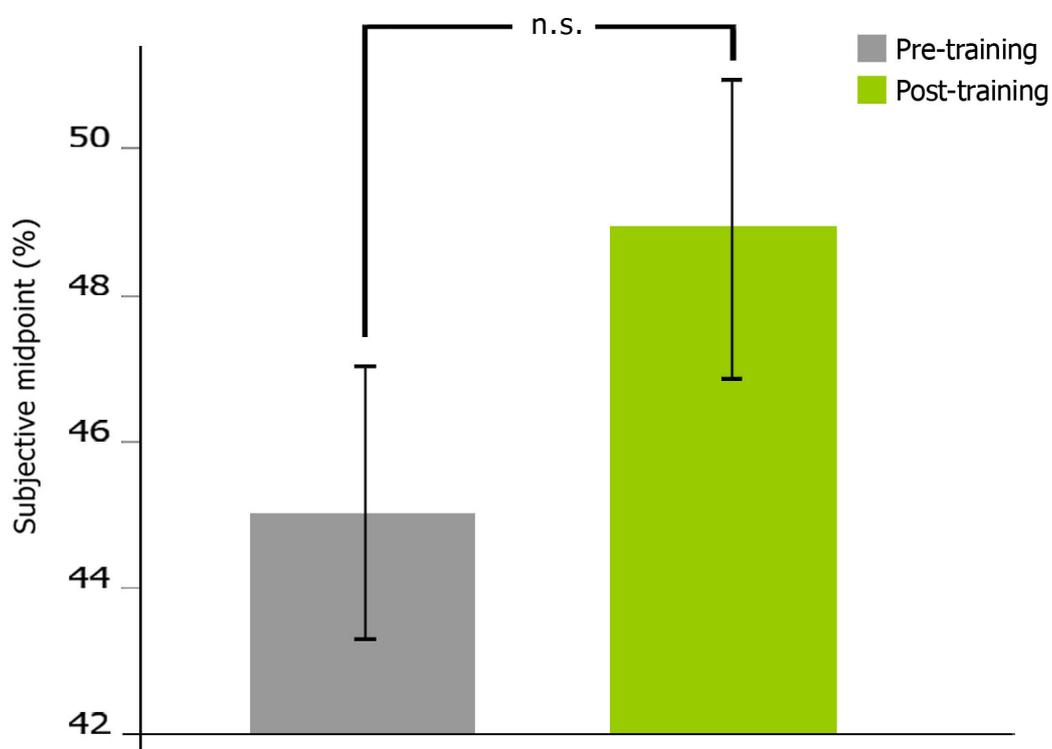


Fig. 4.7 Mean subjective midpoint (%)

Mean percent subjective midpoint (\pm standard errors) before and after the use of a 20 cm-long tool.

This finding shows that the length of the tool, and thus the degree of extension of the reachable far space, seems to be crucial in order to extend the subjective representation of one's own arm length, and hence to determine a dynamic change into the spatial metric representation of body parts.

4.4. Experiment 6

In Experiment 6 we sought to replicate the result of experiment 5, extending the investigation in two directions. First, in this study it was investigated whether the representation of the dominant arm was more prone to be modified by tool use relative to the non-dominant one, being more often used to manipulate tools. Many studies on tool-use in humans have been conducted using the dominant arm (e.g., Bonifazi et al., 2007; Cardinali, Frassinetti et al., 2009; Farnè et., al, 2005). Although there is evidence for tool-dependant modification of body representation after tool manipulation with the non-dominant hand (Maravita, Clarke, Husain, & Driver, 2002). Furthermore, in Experiment 5 no measures of proprioception were taken. As such, the possibility that the distal shift in the bisection task following the training was due to a drift of the perceived position of the whole arm away from the body (i.e. towards the direction of the actions performed during the training) cannot be excluded. Therefore, in Experiment 6, a proprioceptive matching task was also included (see paragraph 4.4.1.2.).

4.4.1. Materials and methods

4.4.1.1. Participants

Twelve volunteers (9 females and 3 males; mean age: 31; mean educational level: 15 years) participated in the study. All but one were right-handed. All the volunteers gave their informed consent according to the Declaration of Helsinki (BMJ 302 (1991) 1194).

4.4.1.2. Experimental procedure

The experimental procedure was exactly the same as in experiment 5 except for the fact that each participant performed the experiment in two separate sessions, using alternatively the dominant or the non-dominant hand. The order of the sessions was counterbalanced between participants. Furthermore, a proprioceptive matching task was included with the aim of estimating the perceived position of the trained arm in the radial plane. Participants were blindfolded and, after each block of bisections (i.e., after the pre-training block and the post-training block), were asked to mirror the position of the trained arm (left or right depending on

the session) with the opposite one (see Fig. 4.1 b). The importance of matching the posture of the entire arm, including the angles of the wrist, elbow and shoulder, was emphasized. Over the wooden boards on which the arms were placed a paper rule was applied, with the 0-cm point at its distal edge. Following task completion by the participant, the experimenter measured the distance of the tips of the two middle fingers from the edge (i.e., the *d value* in the formula reported below); afterwards the difference between these two values was calculated, indicating the extent of the mismatch between the real and the perceived location of the trained arm, according to the following formula:

$$\text{Mismatch} = (d_{\text{untrained arm}} - d_{\text{trained arm}})$$

A positive value indicated that participants perceived their arm closer to their body, relative to its actual position; vice versa, a negative value indicated that they perceived their arm farther from their body, relative to its actual position. The amount and direction of the mismatch before and after the training has been compared by means of a paired t-test.

4.4.2. Results

As shown in Fig. 4.8, Experiment 6 overall confirm the main finding of Experiment 5, namely that participants bisect their arm more distally after the use of a 60 cm-long tool, as if the tool was incorporated into their arm representation.

A repeated measures ANOVA was performed with two main factors, Trained Arm (Dominant; Non-dominant) and Session (Pre training; Post training). Only the main factor Session reached the significance [$F(1,11)=7.58$; $p<0.05$, $\eta^2=0.12$], while neither the factor Trained Arm [$F(1,11)=0.92$; $p=n.s.$, $\eta^2=0.05$], nor the interaction Session by Trained Arm [$F(1,11)=0.34$; $p=n.s.$, $\eta^2=0.001$] were statistically significant. Thus it seems that both the spatial metric representations of the dominant and the non-dominant arm are equally prone to be dynamically modified by tool use (e.g., Maravita, Clarke et al., 2002).

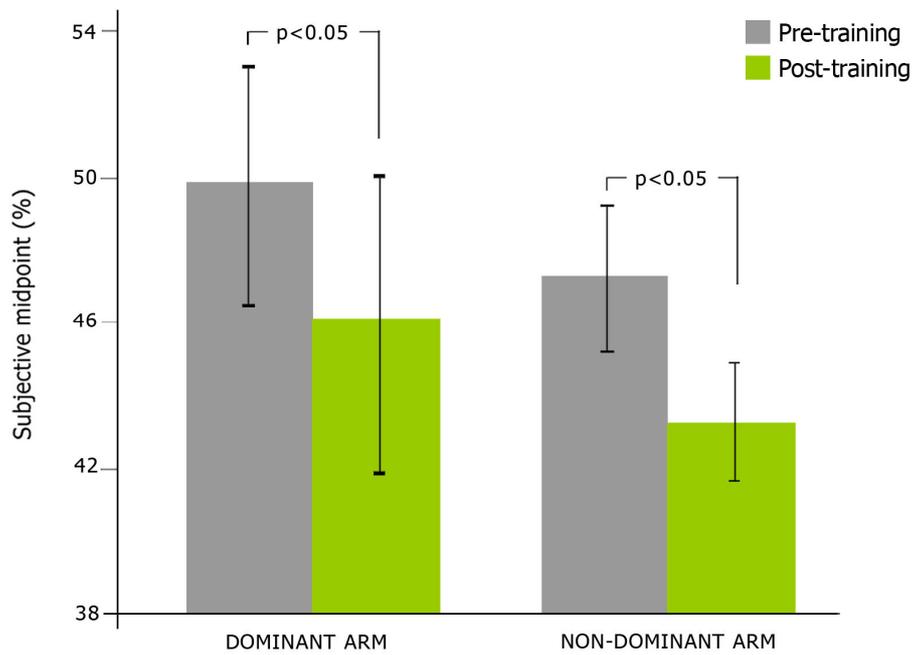


Fig. 4.8 Mean subjective midpoint (%)

Mean percent subjective midpoint (\pm standard errors) before and after the use of a 60 cm-long tool with the dominant and the non-dominant hand.

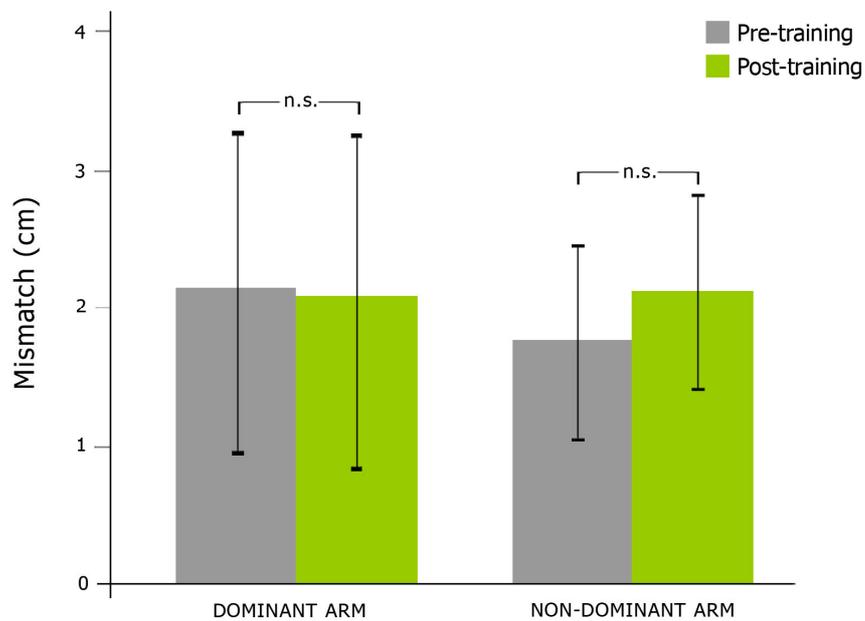


Fig. 4.9 Mean proprioceptive mismatch

Mean proprioceptive mismatch (\pm standard errors) of the trained arm before and after the use of a 60 cm-long tool.

Additionally, the proprioceptive mismatch between the pre- and the post-training sessions was analyzed by means of paired t-tests for each arm. As shown in Fig. 4.9., overall participants made a slight error in the position matching task, indicating that they perceive their trained arm slightly closer their body relative to its actual position; however this trend does not show any difference after the training, thus meaning that the tool use did not cause any illusory proprioceptive misplacement of the whole arm (dominant arm: 2.11 vs. 2.08; $t(11)=0.08$; $p=n.s.$; non-dominant arm: 1.78 vs. 2.11; $t(11)=-0.85$; $p=n.s.$) and hence confirming the validity of the result of Experiment 5.

4.5. Discussion

According to Cardinali and colleagues, so far tool-incorporation has been demonstrated indirectly through perceptual changes in the extent of the peripersonal space (Farnè et al., 2005; Farnè & Làdavas, 2000; Maravita et al., 2001; Maravita, Spence et al., 2002) and cortical correlates of motor imagery (Fourkas, Bonavolontà, Avenanti, & Aglioti, 2008), while no direct evidence of direct modification of the body schema has been reported (Cardinali, Frassinetti et al., 2009). Overall, the findings of Experiments 5 and 6 show that the spatial metric representation of body parts can be modified by the use of a functional tool, compatibly with the spatial representation of a longer arm. Additionally, it seems that the length of the tool and, possibly, the extent to which action capability is enlarged is a critical factor to determine consistent plastic changes. This latter finding seems to be in contrast with a previous study of Farnè and colleagues (Farnè et al., 2005), in which they found similar results using a 60 cm-long modified rake with the functional part placed at 30 cm away from the participant's hand and with a 30 cm-long standard rake. In particular, they found that the tool-use effect on the amount of crossmodal extinction, measured at 60 cm from the patients' body, after the use of the 30 cm-long rake was weaker than after the use of the 60 cm-long tool, but still significant. Conversely, in the control study briefly presented in paragraph 4.3.2. no effect of the training with a 20 cm-long tool was found on arm bisection. It seems that, in the present study, the short rake was not sufficient to induce a modification of the metric representation of the

forearm. There are a couple of reasons for which the contrast between the two studies is maybe only apparent. First, it has to be noted that, even Farnè and colleagues (2005) found a less pronounced effect using the 30 cm-long tool instead of the 60 cm-long one. It may be that, by changing the task and by using an even shorter (20-cm) tool, any residual effect of tool-use was abolished. Second, it may be the case that the space representation in a damaged brain might be more easily changed, while -being more stable in the unimpaired brain- a stronger manipulation is needed in order to obtain similar effects in healthy participants. Moreover, it might be hypothesized that the representation of body parts is more stable than the representation of the peripersonal space, being the body size and shape very stable during the whole adult life. If this was true, one may expect that, in order to induce a modification in the spatial metrics of the body, a relevant extension of the action space by the tool has to be used. On the contrary, as shown by Brozzoli and colleagues (Brozzoli et al., 2009), it seems that, in order to obtain a remapping of the peripersonal space extension, even a voluntary free-hand action is sufficient (see chapter 1 for details about this study). Furthermore, in response to the question about the possible overlapping between the concepts of body schema and peripersonal space (Cardinali, Brozzoli et al., 2009), this putative difference in the plastic properties of the body representation and the peripersonal space representation might be considered as an evidence of independence between these two mental constructs.

Experiment 6 further reinforces the main result of Experiment 5, namely that tool-use can generate an increase in the metric representation of one's own body (arm). Furthermore the present experiment excluded that such an effect could be due to an illusory proprioceptive distal misplacement of the whole arm, and it shows that the spatial metric representation of the dominant and the non-dominant arms share similar plastic properties. Ridding and Flavel have recently reported a related finding showing that reorganization in functionally relevant motor circuits is equally inducible in both the dominant and non-dominant motor cortices (Ridding & Flavel, 2006). In particular, they used the paired associative stimulation paradigm (PAS)⁷ to

⁷ Paired suprathreshold peripheral electrical nerve stimuli and TMS were applied at 0.05 Hz for 30 minutes. Electrical stimuli were delivered to the median nerve and TMS was applied over the optimal scalp

induce motor cortical plasticity (Stefan, Kunesch, Cohen, Benecke, & Classen, 2000) and test the hypothesis that a reduced short-interval intracortical inhibition (SICI) in the dominant hemisphere could facilitate the use-dependent plasticity in the dominant motor cortex (Ilic, Jung, & Ziemann, 2004). They found that PAS-induced excitability changes are similar in the two hemispheres and, additionally, that the performance improvement on a ballistic motor training task (i.e., quick thumb abductions paced by an auditory stimulus) was greater for the non-dominant hand. Thus, their findings do not support the hypothesis that a reduced SICI in the dominant hemisphere could increase use-dependent plasticity in that hemisphere. More interestingly, relative to the findings reported in this thesis, is the fact that these authors did not find any difference in the plastic properties of the motor representations of the dominant and the non-dominant hand, compatibly with the behavioural results of our Experiment 6 where no significant difference in the possibility to induce dynamic changes in the spatial metric representations of the dominant and the non-dominant arm was found.

In conclusion, in addition to the stable representation shown in Experiments 1-2, Experiment 5 and 6 showed that the spatial metric representation of the body is also characterized by plastic properties. It is reasonable to suppose that this plasticity must have a functional aim. On the contrary, one cannot explain the reason why the representation of our body should be modified so rapidly and easily. In this respect, the study by Cardinali and colleagues (Cardinali, Frassinetti et al., 2009) showed that the training with a mechanical grabber produces an after effect on the kinematics of the transport phase of free-hand reaching movements, but it does not affect either the precision of the free-hand grasping or the molar structure of the free-hand movement. Thus, the changes occurring at the level of the body schema do not hamper the accuracy and the successful control of the action; on the contrary, it's reasonable to conceive that the final aim of this dynamic modifications is to obtain an efficient movement programming of action performed with tools in the far space and represent a behavioral consequence of skillful motor learning. In other words, the hypothesis is that an embodied tool, namely a tool

site in order to evoke MEPs in the APB (abductor pollicis brevis) muscles. It is known that the amplitude of the MEPs in APB are increased after PAS.

which is incorporated into the representation of the own body as an extension of the real effector, could be controlled more efficiently and precisely. The question of embodiment is even more interesting in the case of prosthetic arms replacing a missed limb. Indeed, it seems reasonable to think that the possibility to exert an efficient control on the artificial arm is an important requirement in order to subsequently accept it as part of oneself. In this respect, a good functioning of the prosthesis has been found to be related with higher levels of overall satisfaction with the prosthesis itself and with a lower incidence of body image disturbances (Murray & Fox, 2002). Interestingly, differences in prosthesis embodiment are reported between patients using different types of prosthesis. For example those who use a cosmetic prosthesis (as opposed to a functional one) are less able to perform motor imagery of the hand during a hand recognition task, reinforcing the fact that functional tools are better incorporated into a dynamic body schema (Nico, Daprati, Rigal, Parsons, & Sirigu, 2004). Furthermore, as anecdotally reported by several amputees who wear a functional prosthesis, the awareness and attention needed for prosthesis use diminishes over time. It thus seems that a dynamically used prosthesis can be incorporated into the body schema, producing a coherent internal model of the body (Murray & Fox, 2002). According to De Preester and Tsakiris, the question of prosthesis embodiment is definitely wider than the phenomenon of body-extension achievable with tools (De Preester & Tsakiris, 2009). Indeed, the incorporation of such a special tool involves additional emotional aspects, possibly determining also a change in the sense of body-ownership. However, it can be conceivable that, in order to obtain a full acceptance of the prosthesis into the patient's own body and self image, that in a sense represents the final aim of the whole process, a critical requirement might be represented by the inclusion of the prosthetic limb into the spatial and sensorimotor representation of the body.

CHAPTER 5

GENERAL DISCUSSION

Our body is definitely a special object for the brain, being at the same time the physical seat of our subjectivity and a physical entity holding a spatial position in the surrounding space, as any other non-corporeal object. Thus, it's not surprising that the issue of its mental representation has interested, since the end of the nineteenth century just to say about the modern times, several philosophers and scientists. A part from the early speculations (Munk, 1890; Wernicke, 1906), the first conception of a body representation as a spatial and topographical representation of the body in space was introduced by Bonnier. He referred to a spatially organized image of body parts in the external space, rather than to a concept of body representation as a mere feeling of existence, or as a mere consciousness of having a body (Bonnier, 1905). In particular he first introduced the term "body schema" which, afterwards, has been extensively used in the classical neurology and in the neuropsychological literature, not always referring to the same concept (de Vignemont, 2010; see Chapter 1 for a detailed discussion). A widely accepted taxonomy concerning the existence of multiple body representations suggests a subdivision into the two main concepts of a *body schema*, comprising sensorimotor representations that are useful to guide actions, and a *body image*, consisting in all the other perceptual, conceptual and emotional body representations, which are not directly involved in movement execution (Dijkerman & de Haan, 2007; Gallagher, 2005; Paillard, 1999; Rossetti et al., 1995). Other authors suggested a further subdivision within the concept of body image, distinguishing a *body structural description*, defining the relation between distinct body parts, such as their boundaries and their positions relative to each other and a *body semantics*, described as a linguistic and conceptual representation depicting the functionality of body parts and their categorical belonging (Corradi-Dell'Acqua & Rumiati, 2007). Besides the fact that the complexity of the issue did not help the definition of a clear and

shared taxonomy, it has to be noted that different groups of research adopted a different point of view, focussing on different aspects of the question. Thus, while some authors investigated the mere sensory and motor processes connected to body representation (Downing et al., 2001); others focussed on the study of its dynamic properties (Cardinali, Frassinetti et al., 2009; Farnè et al., 2007) and its relationship with space processing and action programming (Brozzoli et al., 2009). At an higher level also the sense of body ownership (Tsakiris et al., 2008; Tsakiris & Haggard, 2005; Tsakiris, Hesse et al., 2006; Tsakiris et al., 2010; Tsakiris, Prabhu et al., 2006) and the sense of the self (Devue & Brédart, 2010; Gillihan & Farah, 2005; Sugiura et al., 2006) have been studied.

This thesis investigated the existence of a spatial metric representation of the body, trying to answer the following questions:

- 1) Are there any differences in the spatial analysis of the metric properties of bodily and non-bodily objects?
- 2) Can the body metrics be used to scale the extrapersonal space?
- 3) Is the metric representation of body parts stable or functionally modifiable?

Concerning the first question, Experiment 1 demonstrated that discrete and independent mechanisms may control the spatial processing of the length of corporeal relative to extracorporeal objects, with the former having a more stable metric representation. In particular it was shown that Unilateral Spatial Neglect (USN) may affect to a different extent the spatial analysis of body parts relative to extrapersonal three-dimensional objects. Indeed, USN patients showed a significant smaller rightward deviation score in the bisection of their own forearm, relative to the bisection of a length-matched cylinder. Interestingly, the same advantage in the spatial processing of a body part, relative to a non-bodily object, emerged in the control group. Besides this main pattern, showing a benefit in the spatial analysis of the metrics of body parts, two patients exhibited an opposite advantage in the solid bisection, thus suggesting the possibility of a double dissociation.

Experiment 2 further specifies the main result obtained in Experiment 1, asking healthy volunteers to perform the same bisection task in three different target conditions (real forearm,

fake forearm and cylinder) using alternatively the right or the left index finger. Overall, Experiment 2 showed similar mechanisms of spatial analysis for bodily objects, either real or fake, compared to non-bodily objects. Moreover an external variable, such as the hand used to perform the task, influenced only the performance in the cylinder bisection, leaving unchanged the performance in the forearm and fake forearm conditions. Thus, these results suggest the existence of a quite stable metric representation of body parts that would act as a reference point, making the performance more stable and not open to the influence of such external variables. Moreover, it seems that the advantage emerged for the body in Experiments 1 and 2 can be explained by the activation of a visuo-spatial representation of the prototypical shape of the body and that coding the length of body parts and of extrapersonal objects are dissociable functions. Even from a more theoretical point of view it seems conceivable to hypothesize the existence of a metric representation of the body; indeed, as suggested by Longo and colleagues, a model of body size and shape is necessary in order to perceive the metric properties of objects touching the skin, as well as in order to localize the spatial position of our body parts (Longo et al., 2010). Concerning the first point, these Authors suggest that people are able to perceive the size of an object touching a single skin surface on the basis of the extent of the portion of the skin that is touched by the target object. In order to do that a reference to a representation of the size of the body part touched is needed; so for example they state that *"if I feel that an object covers half the width of my hand, I can only form a representation of the object's size if I know how wide my hand is"* (Longo et al., 2010; p. 659). Relative to the second issue, they suggest that in order to localize the position of a body part in the external space a combination of postural information (joint angles) and information about the length and width of the bodily element linking those joints is necessary. Given that any afferent channel is known to provide information about body parts size, a pre-existing body size representation must be hypothesized.

Concerning the second question at the basis of the present doctoral work, Experiments 3 and 4 showed that the spatial encoding of an extracorporeal object (i.e., a cylinder) can be facilitated and can become more efficient, thanks to the presence of the own forearm in the same space

occupied by the cylinder. Thus, it seems that in this latter case participants can implicitly rely on a well known metric representation of the forearm to estimate the length of the cylinder. This result, extending previous findings about the possibility to use body parts length as an intrinsic metrics to determine the boundary between near and far space (Longo & Lourenco, 2007), further suggests that the metrics of body parts actively scale the metric judgement relative to objects they manipulate, in an online, continuous manner.

Furthermore, Experiment 3 calls for the importance of proprioceptive information in the automatic coding of the body metrics, given that the presence of the forearm in a given space sector in which a metric judgment relative to an extrapersonal object is required, improved the performance even if the forearm was out of visual control. Actually, a strict relation between the availability of coherent postural information and the stability of the representation of the body, as an extended object in space, has been already demonstrated (Longo et al., 2009). Experiment 4 further investigated this issue, testing whether the availability of a well-working somatosensory-proprioceptive system is necessary to allow the use of the spatial metric representation of body parts as an implicit metric system, useful for example to better evaluate the length of a non corporeal object. The results showed that the possibility to rely on a spatial metric representation of the body as a reference for the spatial coding of extrapersonal objects, sharing a common space with the body, is based on the availability of efficient tactile and proprioceptive information. Thus, Experiments 3 and 4 clearly favour the hypothesis that an ongoing spatial metric representation of body parts exists, and it can be implicitly used to scale the size of extrapersonal objects in the external space. Moreover, it seems that it can be critically altered by cerebral lesions even if it's not yet clear whether the distortion is relative to the metric representation itself or the afferent input necessary to build up such a representation.

In the second part of the present thesis the dynamic properties of the metric representation of body parts were investigated, hypothesizing that besides being stable, a useful model of body size must be also functionally modifiable under certain conditions. Thus, concerning this last question, Experiment 5 demonstrated an extension of the metric representation of the arm, as

a consequence of extensive tool use. In particular, the expert and prolonged use of a tool extending the reachable space, bias the radial bisection of the forearm towards its distal end, compatibly with the feeling of holding a longer arm. It is indeed conceivable that an extension of the action space, by means of a functional tool, produces a change in the representation of the arm length, with the final aim of exert a more efficient control over the action performed with the tool. Indeed, as reported in a recent study (Cardinali, Frassinetti et al., 2009), tool-use induced modification at the level of the body schema do not affect the precision and the molar structure of the subsequent free-hand grasping, even if changes the parameter of reaching compatibly with the representation of an elongated limb. On the contrary, it is reasonable to conceive that if a tool is incorporated into the representation of the own body, as an extension of the real effector, then it can be more efficiently and precisely controlled.

Furthermore, it seems that the length of the tool is a critical variable in order to determine a change in the metric representation of the arm, possibly because the effect depends on the extent to which action capability is extended. Indeed, no consistent plastic changes were found in a control study in which participants were trained with a 20 cm-long, instead of a 60 cm-long, functional tool. On the contrary, it was shown that a voluntary free-hand action is sufficient in order to obtain a remapping of the peripersonal space extension (Brozzoli et al., 2009), thus indicating a difference in the plastic properties of the body and the peripersonal space representations that might be taken as an evidence of independence between these two mental constructs (Cardinali, Brozzoli et al., 2009). Experiment 6 reinforced these findings showing, by means of a control task, that the lengthening in the metric representation of the arm was not due to an illusory proprioceptive distal misplacement of the whole arm. Moreover, it demonstrated that the spatial metric representations of the dominant and the non-dominant arms share similar plastic properties, being both equally prone to be modified by tool use (Maravita, Clarke et al., 2002; Ridding & Flavel, 2006).

Starting from these evidence, several other questions might be investigated in future studies. For example, one may wonder if the features of the body metric representation change during the development; indeed, as noted by Longo and colleagues it can be hypothesized that the

clumsiness of movements, typically seen in adolescents, often supposed to be related to the rapid changes in body size due to the “growth spurt”, is the consequence of a delay in the updating of the body model consistently with modifications of the physical body (Longo et al., 2010). In this sense, one open question is whether the body metrics is less stable in adolescence than in adulthood. On the other side, concerning the dynamic and plastic properties of the metric representation of body parts, it would be interesting to know how long the effect of a tool training lasts. In this respect, relatively long lasting effects were demonstrated to occur in the damaged brain after the extensive use of a rake, with the crossmodal extinction rate coming back to its baseline 90 minutes after the end of the training (Maravita, Clarke et al., 2002). However, given that plasticity should have a functional aim, it is reasonable to suppose that the effect of a novel tool-use training in a healthy brain doesn't last so long. A distinct question is the durable effects induced by long-term everyday life experience of tool use, such as for example the use of the cane in blind people (Serino et al., 2007) or the use of a functional prosthesis in amputated patients. Even if the question of tool embodiment is definitely wider, including for example emotional and higher-level cognitive aspects (De Preester & Tsakiris, 2009), it can be supposed that, in order to facilitate the acceptance of a prosthetic limb, the possibility to intentionally and efficiently control the artificial arm is an important requirement to subsequently generate a feeling of ownership. As already mentioned in Chapter 4, interesting differences emerged between people wearing a functional, rather than a cosmetic, prosthesis, emphasizing the fact that functional tools are better incorporated into a dynamic body schema (Nico et al., 2004).

Such a change in the feeling of ownership, would be likely to be long-lasting. Furthermore, acquiring tool-use skills in humans in other conditions may also show long lasting effects, given, for example, the generalization that any training could generate for further experience, even with slightly different tools. It is in facts conceivable that the human brain is capable of generalizing the motor patterns acquired during a certain training and exploit them in the case of a novel situation. This hypothesis is surely worth future experimental work.

In conclusion, the main findings reported in this doctoral work showed that body size holds a stable mental representation (Experiments 1-4), being at the same time characterized by an extraordinary plasticity (Experiments 5-6) as a function of the environmental aims that the body is called to fulfill in everyday situations.

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