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BODY SCHEMA PLASTICITY AFTER TOOL-USE

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Abstract

We all have a body: our own body and just one body. Through it, we move, we interact with the world and other persons, we perceive, basically we live. It's a unique essential object. If it is true that we have only one physical body, we also have many representations of it in the brain.

There is little agreement about the exact number of body representations in the brain, but not on the fact that we have more than one. The multi-componential models of body representation are based on the notion, supported by scientific evidence that different activities demand and rely on specifically adapted representations.

In my thesis, I studied one particular body representation that is used and involved in action planning and execution, i.e. the Body Schema.

I have been able to describe and measure the plasticity of the Body Schema and its level of specificity in healthy individuals. In particular, using a tool-use paradigm, I showed that the Body Schema is quickly and efficiently updated once a change in the body configuration occurs. With a series of kinematic studies, I contributed unveiling the ingredients that rule the plasticity of the BS and the sensory information that is used to this purpose.

As a result of my thesis, I suggest that a clearer definition and operational description of the Body Schema, as an action-devoted repertoire of effectors representations, is possible, particularly thanks to its plastic features.

From the body to its representation(s)

News from the body

Satisfaction of each fundamental need and preservation of life require an action or series of actions: Eating, drinking, reproducing, avoiding threats etc. To efficiently act means to make our body moving in the most correct and efficient possible way in order to achieve the desired goal. This implies a precise and ready-to-use knowledge of the configuration, shape and position in the space of our own body. If I want to grasp a glass of water to drink, I need to know the position in space of the glass, as well as (1) the position of my hand to implement the good trajectory, (2) the length of my arm to decide whether I have to approach the trunk to the target or not, (3) the shape of my hand to decide if I have to stretch my fingers, or rather close them. All that information initially comes from peripheral receptors[1], which provide signals that, through specific pathways, reach the thalamus and the cortex where they are processed and integrated into a representation of the body the brain uses to plan and execute actions which has been called Body Schema. That's why, before going through the history of the body representation, I will briefly recall some basic notions about the organization of our somatosensory system, as it is via the afferent information from the periphery to the cortex that the brain is informed of the actual state of the body. Many different sub-modalities convey inputs through this system to

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[1] The somatosensory system conveys information about muscles contraction or extension, joint flexion and skin stretch. This proprioceptive information informs the brain about the position and configuration of the body parts. As it has been recently pointed out (Longo et al, 2010) there is no signal that informs the brain directly about the size of a body part. This knowledge must be, as a consequence, represented in a stored representation of the body. The issue of the metric of the body representations is of great importance for this dissertation and will be addressed in chapter 2.

the cortex, in a topographically organized manner, and they can play different roles in the updating and feeding of the Body Schema (hereinafter, BS).

The human somatosensory system

The electrophysiological study of the somatosensory system began in 1925 with the recording of action potentials from fibers of muscles spindles in a frog by Adrian and Zotterman (Adrian and Zotterman 1926a; Adrian and Zotterman 1926b). Using a capillary electrometer they showed that, when applying different weights and so stretching the muscles to different extent, several impulses were generated by the receptors at a particular frequency, which increased with the load and decreased with the time of application. This important study and those who came after contributed to the knowledge of the somatosensory system and in particular to the Johannes Peter Müller's theory of sensation, according to which an evoked sensation depends on the sensorial organ and not on the stimulation mode itself. The same electrical stimulation applied to different nervous fibers, for example the optical nerve and the auditory nerve, will produce a different sensation, in our example visual and auditory. It is the type of the fiber stimulated, and the cortical area the fiber is connected to, that determines which sensation will be evoked and not the stimulation by itself.

The somatosensory system provides four different modalities: touch, proprioception, nociception and temperature. Each of those sensations is mediated via specific receptors and pathways which activation determines the evoked sensation.

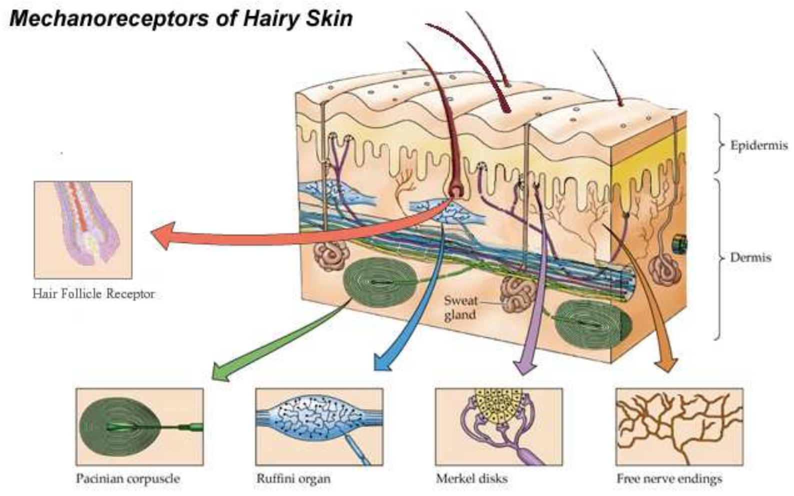
In the present paragraph I will focus only on touch and proprioception pathways as they are considered of major importance in the updating of the Body Schema.

Touch

Touch, as well as proprioception, is mostly mediated by nerve ending embedded in specialized capsule. Mechanoreceptors of the glabrous skin are divided in two classes: deep receptors and superficial receptors (Figure 1).

Superficial receptors are Meissner corpuscle and Merkel cells. They are both situated in the superficial layers of the skin and mediate light touch, texture discrimination and pressure. Meissner corpuscles are rapidly adaptive receptors with a high sensitivity (low threshold) due to their particular position within the dermal papillae.

They are activated when light touch is delivered and rapidly generate action potentials, which quickly decrease and eventually disappear if pressure is maintained constant. When the stimulation is removed, the corpuscle regains its original shape causing a second volley of action potentials that inform the brain about the end of the stimulation. Merkel cells are rather slowly adapting receptors and show sustained response to prolonged mechanical deflection and displacement of the tissue. Deep receptors include Pacinian and Ruffini's corpuscles. They are bigger and less numerous than the superficial receptors. Pacinian corpuscles have a structure similar to Meissner's ones, with which they share also the characteristic of being rapidly adaptive receptors. They respond to the dip of the skin, without providing any response to stationary pressure. They can be activated by vibratory stimulations even when they are applied few centimeters far away from the corpuscle location at a specific frequency (200-300 Hz). Ruffini's corpuscles are slowly adapting receptors that are sensitive to skin stretch. All these structures contain the peripheral ending of neurons, whose cell body is located in the dorsal root ganglions, who carry out two important functions: the stimulus transduction and the retransmission of stimulus



courtesy of http://www.hhp.uh.edu/clayne/6397/Unit4_files/image019.jpg

Figure 1. Somatic sensory receptors of the hairy skin.

information to the central nervous system. Mechanoreceptors are innervated by neurons with large myelinated axons, which allow a fast retransmission of the signal (35/70 meter/second). Each neuron has a receptive field that depends on the type and location of the innervated mechanoreceptor. For example, fibers that innervate superficial mechanoreceptors receive information from many receptors (10-25 Meissner corpuscles) with a receptive field that can extend for 2-10mm. At the contrary, deep receptors are separately innervated by one fiber and have much larger receptive fields (a Pacinian corpuscle of the hand can display a 10 cm-wide receptive field). This confers diverse properties to the receptors, the superficial ones being able to carry out fine discrimination of the stimulus properties, whereas deep receptors can resolve only rough differences. Another interesting aspect is that the distribution of these receptors varies across different body-parts, resulting in a difference in sensory acuity. For example, in humans the smallest receptive fields are in the fingertips, where the concentration of Merkel's and Meissner's corpuscle is particularly high, and their size increases along the proximal direction (figure 2).

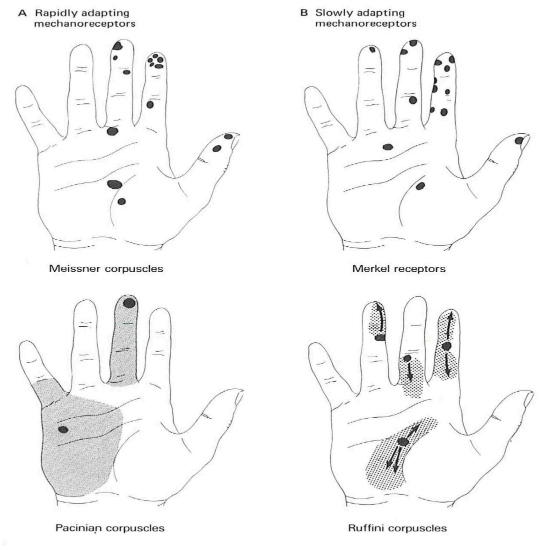


Figure 2. Location of some mechanoreceptors in the glabrous skin of the hand and size of their receptive fields.

From Kandel et al., 2000

Proprioception

Proprioception is the sense of the static position (statesthesia) and movement (kinesthesia) of the body-parts, which allows us to appreciate posture changes even in the absence of visual information. Three types of mechanoreceptors provide proprioceptive information[2]. The receptors of the muscle spindle are situated in the belly of a muscle and provide the CNS with information about changes in the length of the muscle itself. The Golgi tendon organs are located at the insertion of skeletal muscle fibers into the tendon of skeletal muscle. They register and transmit information about the amount of contraction of the muscles. Finally, the receptors of the joint capsule are sensitive to the flexion and extension or articulation. Together, they provide the brain with the relevant information to decide about the flexion/extension of a particular muscle, the strength of the movement and it's velocity. As for the mechanoreceptors of the skin, those receptors are innervated by large myelinated fibers that assure a fast transmission of the signal (see table 1).

FIBER	**INFORMATION**	**SIZE**	**VELOCITY**	**RECEPTORS TYPE**
Aα	Proprioception	large myelinated	70-120 m/s	Muscles spindles Golgi tendon organs
Aβ	Proprioception	large myelinated	35-70 m/s	Muscles spindles
	Touch			Meissner and Merkel corpuscles (type 1) Pacini and Ruffini corpuscles (type 2)

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[2] Mechanoreceptors of the skin too contribute to the sense of body parts' position by informing the cortex about the stretch of the skin (Edin, 1992).

Dorsal column-medial lemniscal pathway (DCML)

The DCML pathway is characterized by three level of retransmission of the information since three sensory neurons are connected. The first neurons of the chain are the ganglion neurons innervating the peripheral receptors. Already at this stage, a topographical organization can be observed. The skin areas innervated by fibers from one dorsal root (dermatome) are organized in a caudal-rostral manner (figure 3). This spatial segregation is the reason why even a central lesion can affect a relatively circumscribed part of the body, as in the case of deafferented patients that will be described in the next paragraph.

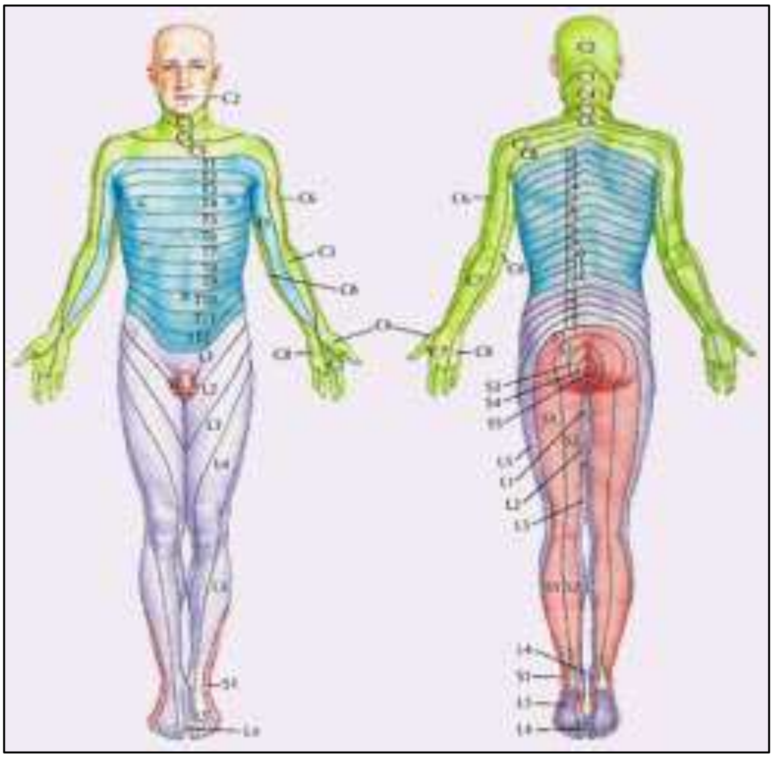

Figure 3. Schematic representation of dermatomes.

In the spinal cord, the large fibers conveying tactile and proprioceptive information follow a different pathway with respect to the smaller fibers (conveying thermal an noxious information). The axons of the ganglion cells continue inside the spinal cord, running up the posterior (dorsal) columns. Axons from the lower body are located most medially (closer to the midline), and run in the gracile tract of the spinal column.

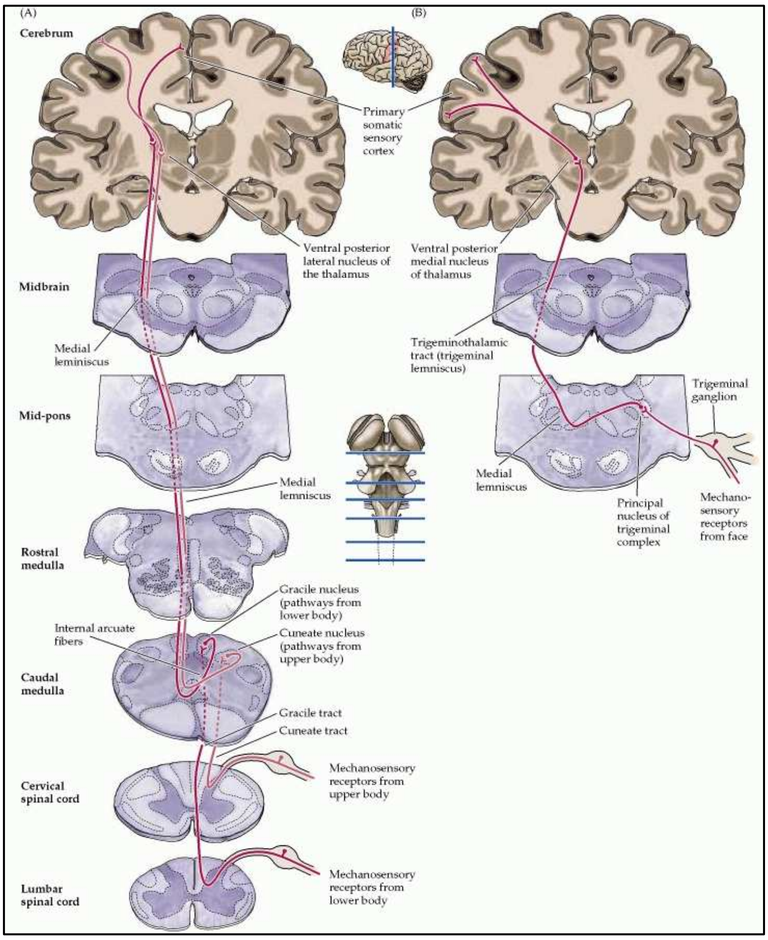

Figure 4. Schematic representation of the DCML system

Sensory axons from the upper body enter the spinal cord later, specifically from the thoracic segment T6 on up (see figure 4). They are therefore disposed more laterally and travel up the cuneate tract.

Axons of the both tracts, cuneate and gracile, end in the homonymous nuclei, where a second synapsis is made. Then the axons cross the midline to ascend contralateraly to the represented body side. The third neurons have their body in the thalamus. The thalamus is not just a retransmission structure, since a first processing is done in its nuclei. The thalamus is a structure of the diencephalon composed by nuclei that have distinct connections to the cortex depending on the type of sensory information they process. In the ventral posterior part there is the relay of the somatosensory information from the periphery to the cortex, and in particular to the primary somatosensory cortex (S1). This part is composed by two nuclei, the ventral posterolateral nucleus (VPL), the ventral posteromedial nucleus (VPM). VPL receives projections from the DCML about the body and projects to S1 in the post central gyrus. The VPM receives tactile, thermal and noxious information about the head and the face area via the 5th cranial nerve. In both nuclei a somatotopic organization has been observed (Lenz et al 1988).

The Somatosensory cortex

The somatosensory cortex is divided in two parts, the primary somatosensory (SI) and the secondary somatosensory cortex (SII). They are both situated in the anterior portion of the parietal cortex (APC) (see figure 5). SI occupies the post central gyrus, just behind the central sulcus.

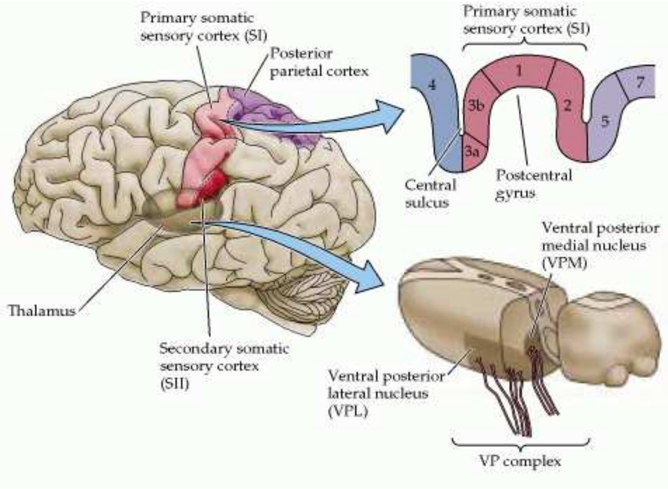

Figure 5. Schematic representation of the Primary (light pink) and secondary (dark pink) somatosensory cortex. The thalamus and the posterior parietal cortex are also represented

It is composed by Brodmann areas 1, 2 and 3 that differ for their structure, function and type of afferent input.

Area 3 has been divided in two sub areas. Area 3a lies in the fundus of the central sulcus, and area 3b in the rostral bank of the postcentral gyrus. Area 1 lies on its crown and reaches down into the postcentral sulcus and caudally to it is located area 2 (Geyer, Schleicher, and Zilles 1999). These four areas receive inputs from the periphery in such a way that in each of them one modality prevails over the others. In particular, 3a receives afferents from muscles spindles and it is responsible of hard vs. soft, roughness and convexity of the stimulus processing; 3b from cutaneous receptors (both rapidly and slowly adapting receptors) and is involved in tactile discrimination tasks. Area 1 receives input from rapidly adapting receptors of the skin and is sensitive to movement and direction, and finally area 2 receives input from deep pressure and joints receptors (Geyer, Schleicher, and Zilles 1999). Thalamic projections from VP enter the cortex at the level of the IV layer from which the information is transmitted to the others layers. Area 3b receives the majority of the projections from the thalamus and its surgical removal produces an inactivation of area 1 with which it is highly interconnected (Garraghty, Florence, and Kaas 1990).

Each area has its own somatotopy, which means that a complete representation of the contralateral half of the body surface is present (J. H. Kaas 1993). Penfield and colleagues (Penfield and Boldrey 1937; Rasmussen and Penfield 1947) using a technique of cerebral stimulation first described what is now widely known as somatosensory homunculus.

These maps follow a common type of organization: the body is represented in a caudal-rostral direction in a mediolateral sequence. The leg and trunk representation is located medially in respect to the hand and the face (see figure 6). In 3b two parallel representation are present, one for each adaptation mode, i.e. the fingers are represented in two columns that receives input one from the rapidly adapting and the other from the slowly adapting receptors (J. Kaas et al. 1979; Kandel, Schwartz, and Jessell 2000).

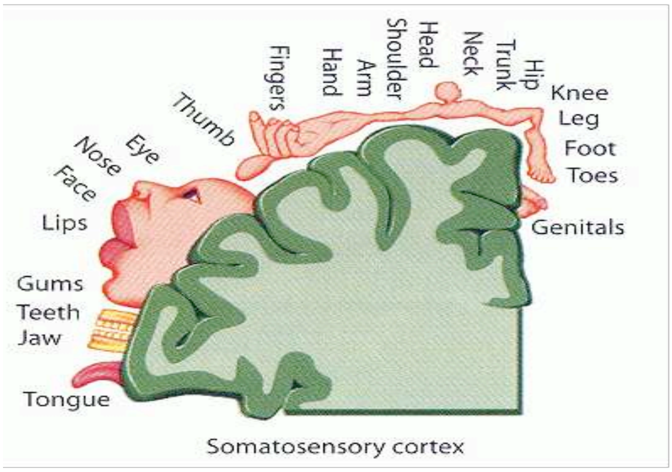

Figure 6. Schematic representation of the somatosensory homunculus in SI.

Moreover, the homunculus is a distorted representation of the body where the amount of neurons and thus of space dedicated to a particular body-part is not determined by its physical dimension, but by the density of receptors. Thus, the hand, the lips and the feet have a larger representation than the legs or the trunk despite their actual size is much smaller.

The four areas of APC are strongly interconnected to each other. In particular, it has been shown that abundant and bidirectional connections exist between area 1 and 3b as well as 1 and 2, organized in a somatotopic way (Burton and Fabri 1995; Pons and Kaas 1986).

S1 has also important connections with higher order areas in the parietal cortex. In particular, reciprocal connections exist between S1 and the secondary somatosensory cortex (SII) where stimuli from both sides of the body are processed. SII has also a greater stimulus selectivity and larger receptive field that allow more complex processing of the stimulus. Two pathways originate from S1: the first pathway goes through area 5 and 7b in the posterior parietal cortex; the second one projects to SII, in the superior bank of the lateral sulcus, which in turns project to the insula. It has been proposed that these two pathways are the analogous of the dorsal and ventral streams of the visual cortex (see p.15-16 of this thesis). In particular, the S1-area5-area7 pathway would be involved in object processing for action planning (Mountcastle et al. 1975) while the S1-SII-insula pathway would be involved in object perception (see p. 20-21 for discussion).

Models of Body Representation

The necessity of having a representation of the body that stores all the information about its configuration is evident and has been formulated more than a century ago by Pierre Bonnier (1905) who first suggested the existence of a spatially organized representation of the body ("spatial sense"). However, Head and Holmes, with their work on Brain (Head & Holmes, 1911), are more often considered as the first authors having proposed an organized model of body representations. In their paper, the authors introduced the idea of the existence of a "Postural Schemata" (later become Body Schema), a representation of the body used for action execution and appreciation of postural changes, separated from a Superficial Schema, devoted to localization of tactile stimulation on the body surface. The dichotomy was mainly based on the performance of a patient (HR) who, after surgical ablation of a portion of the precentral gyrus, was perfectly able to localize a stimulated spot on his hand (naming it or pointing to a model), but failed in reproducing or describing the position of the same hand. The authors observed a deficit in recognizing the position in space of the left affected arm and especially of the distal segments. In particular, the patient was not able to update the representation of the left arm position after passive movement. The lack of proprioception made him develop a visual strategy according to which he formed a visual image of his arm configuration that he was able to consciously update if visual feedback of his own voluntary movements was available. However, in the case of passive movements with eyes closed, the visual image of the arm position persisted unchanged. As a consequence, despite some spared tactile perceptual abilities, touch localization through a pointing movement was impossible for stimuli delivered on the left arm because of the inability to localize the arm itself. Instead, when asked to report verbally, or on a map the position of the stimulation, his answers were correct.

At page 187 of their seminal paper, Head and Holmes wrote:

> *“For this combined standard, against which all subsequent changes of posture are measured before they enter consciousness, we propose the word "schema." By means of perpetual alterations in position we are always building up a postural model of ourselves which constantly changes. Every new posture or movement is recorded on this plastic schema, and the activity of the cortex brings every fresh group of sensations evoked by altered posture into relation with it. Immediate postural recognition follows as soon as the relation is complete”.*

In those few lines, all the main characteristics of the Body Schema were already outlined.

First of all, the Body Schema is a constantly updated representation. This is because our own body is constantly changing at least in position but also, even though in a longer time scale, in dimension throughout the entire life: the motor system needs to be provided with a correct knowledge of body configuration, hence the need to update the BS.

The second main feature of the BS is that the update is done using *“fresh group of sensations evoked by altered posture”*, that is propriocepive, kinesthetic and tactile information. Proprioception in particular it’s thought to play a key role in the plasticity of the Body Schema since it’s the modality that informs the brain about change in spatial configuration of body-parts, through muscles and joints receptors. However, after Head & Holmes’ work, it has been shown that tactile mechanoreceptors can provide additional information about joint configuration (Edin 1992).

Finally, the authors proposed this update to happen at an unconscious level. Indeed, when we start a movement and during its execution, we don’t need to pay attention to our body, as its (change in) position and configuration are already available and unconsciously processed. However, the final result of the updating can be conscious, which means that we can verbalize or be aware of our own body position.

Already in the same seminal paper, Head and Holmes also proposed the existence of a second body representation called Superficial Schemata, which is a conscious representation devoted to perceptual goals. The Superficial Schemata, which has been called Body Image (although not uniformly) in the subsequent nomenclatures, allows for the “recognition of the locality of a stimulated spot”. Its integrity in patient

HR was responsible of his spared ability to localize tactile stimulation with the naming or map task.

This dichotomy still persists, together with the experimental approach used by the authors to test the integrity/deficit of the two body representations. Subsequent studies used motor and perceptual tasks to separately access the Body Schema and the Body Image (hereinafter, BI), respectively. This approach has been widely influenced and motivated by the introduction of the visual two routes model (Goodale and Milner 1992a; Milner and Goodale 2008a) to the somatosensory system and more recently to the body representation domain (Dijkerman and De Haan 2007; Kammers et al. 2009; Kammers, Mulder, et al. 2010)

The two-route model suggests that the same sensory information can be processed in different ways in different brain structures depending on the aim of the individual; two separated, although richly interacting streams, are dedicated to the processing of sensory information when an action (dorsal stream) or a perceptual judgment (ventral stream) is requested. This has been originally shown in the visual domain (Goodale and Milner 1992b; Mishkin and Ungerleider 1982), and then in the auditory (Belin & Zatorre, 2000) and somatosensory domains (Dijkerman and De Haan 2007; Kammers, Longo, et al. 2009).

Mishkin and colleagues (Mishkin 1979; Mishkin and Ungerleider 1982) first suggested the existence of a ventral visual stream (the “what” way) and a dorsal visual stream (“where” way). Both originating from the striate cortex, the two streams then diverge from it and also receive separated projections. Based on a large amount of electrophysiological, anatomical and behavioral studies, they proposed that the two streams differ by the type of information they elaborate. The dorsal stream, reaching the posterior parietal cortex, is dedicated to the processing of spatial information of an object thus its lesion results in the inability to localize the object. The ventral stream, that reaches the inferior temporal cortex, has the function of elaborating object qualities and so contributes to object recognition. Because of their functions, the two routes of this model are also called “where” and “what” stream. Further support from this model came from monkey studies showing a dissociation between object discrimination and object localization. Gross and colleagues (Gross, Rocha-Miranda, and Bender 1972) showed that a lesion of the inferior temporal cortex lead to impairment in a visual discrimination and recognition task but not in a spatial one. The opposite pattern has been observed after lesion of the posterior parietal cortex (Ungerleider and Brody 1977). In Ungerleider and Mishkin's model the dissociation between the two routes is based on the fact that they process different aspects of a same object. This means that no matter what I want or I am asked to do with an object, its position will be elaborated in the dorsal stream while its features, like the color or the shape, will be processed in the ventral stream. Ten years after this first two-route model, Goodale and Milner (1992) proposed a different interpretation for the functions of the two anatomical pathways. In their model, they strengthen the importance of the output and propose a new taxonomy, namely "what" vs. "how". In particular, they suggest the existence of a vision for the perception ("what" route) in the occipital-temporal cortex, and a vision for action ("how" route) in the occipital-parietal cortex. Putting the accent on the aim of the processing means that the same feature of an object, like its position or its size, will be processed for example in the dorsal stream if I want to grasp that object, or in the ventral stream if I have to recognize it. It is not the type of information *per se* that determines which route is activated, but the goal the processing subserves. Recently, Dijkerman and de Haan (Dijkerman and De Haan 2007) took inspiration from Goodale and Milner's work to interpret the existence of separated cortical pathways for somatosensory information in terms of separated processing streams. Indeed, Mishkin described in the late 70s a somatosensory pathway running form the anterior parietal cortex (APC) to the insula, via the secondary somatosensory cortex (Mishkin, 1979). Dijkerman and de Haan suggested that this pathway is responsible for recognition and perception of external objects (the "what" way), while the action-related processing (the "how" way) is done through a different cortical pathway that originates in APC and terminates in the posterior parietal cortex (PPC) (see figure 7).

An important characteristic of this model is that stimuli are processed in a sequential way (Inui et al. 2004) so that the more we progress along the pathways the more elaborated is the processing.

However, compared to the other sensory systems, the somatosensory system has the specific and unique feature of providing information not only about the external world but also about the body itself. This two routes model may thus also explain the somatosensory perception of the body itself. As shown in figure 7, the APC-PPC-insula route is proposed as the neural substrates of the perceptual representation of the body (BI), with PPC dealing with the metric aspects of the body and the insula being responsible for the sense of ownership of one's own body. The APC-SII-PPC, on the other hand, codes for the body representation for action (BS).

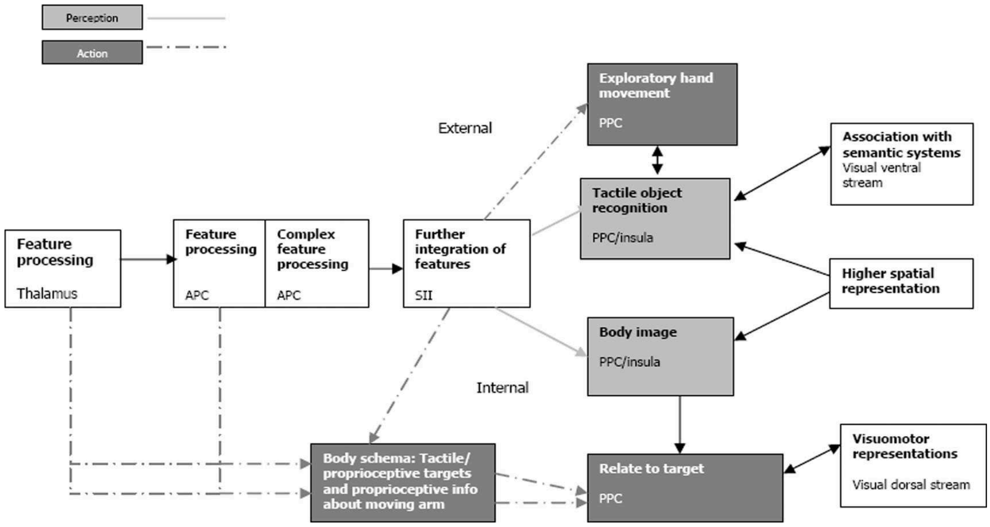

Figure 7. Outline of the two-routes model of somatosensory processing. From Dijkerman and de Haan, 2007

Interestingly, the PPC seems to be involved in both perception- and action-related body processing. As the authors point out in the review, in the somatosensory system the independence of the two routes seems to be less strong than in the visual system. One possible and plausible explanation is that for a correct haptic perception and recognition of an object, information from the perceptual and the action stream has to be integrated in order to create a veridical percept. However, independence of the two streams has been proven and the distinction between body representation subserving action and perception is at the base of the dyadic models of body representation that will be reviewed in the following paragraph.

Dyadic models

Dyadic models postulate the existence of two separated body representations. Most of such models agree in identifying the Body Schema as one of the two representations. The BS is a plastic, action-devoted schema of the body that is built on proprioceptive (and tactile) information, whose update is essentially unconscious. Dyadic models descend directly from Head and Holmes' model presented before and this is particularly true for the description of the Body Schema that was already, in Head and Holmes' theory, described as a motor-oriented representation. The major contribution of the two routes model on the BS has been to provide a new methodological approach to test its characteristics, and dissociation from the body representation for perception, i.e. the Body Image. Different is the case for the BI. Indeed, most of the models also agree on the existence of the Body Image, a perceptual conscious representation of the body. However, if the scientific community almost unanimously agrees on a coherent and structured definition of the BS, the conceptualization of the BI suffered from a lack of characterization. As recently pointed out by de Vignemont (de Vignemont, 2010), p. 670, *"The body image groups all the other representations about the body that are not used for action, whether they are perceptual, conceptual or emotional (body percept, body concept and body affect)",* which means that the name body image has been frequently used for all what the body schema is not, in a sort of by default definition. In this context, the application of the action/perception model had the great merit of helping define the BI, mainly by providing a theoretical and methodological frame for scientific investigation. Dyadic models are indeed based on dissociations observed both in patients and, more recently, in healthy subjects, at different levels.

Following the two-routes model, perceptual and motor tasks have been designed and used to separately access respectively the BI and the BS. This type of approach brought to a dichotomic way to describe the two representations. In particular, three main dimensions can be identified of which BS and BI represent the two extremities (see table 2). The first is the action/perception dimension, already mentioned above. The second one is the level of consciousness, where the BS is considered of as an unconscious body representation and the BI as a conscious one. Finally, the two representations are supposed to differ in terms of temporal dynamics, the BS being a short-term representation while the BI a long term one.

	Body Schema	**Body Image**
Function	Action	Perception
Consciousness	Mainly unconscious	Conscious
Temporal dynamics	Short-term	Long-term

In the following paragraphs, I will present the relevant work that contributed to the characterization of the BS and the BI. In the first paragraph, I will review five neuropsychological studies in which the authors addressed the issue of the dissociation between a body representation for (tactile) perception and a body representation for action. In the second paragraph, I will present more recent studies on healthy subjects on whom sensory illusions have been used to separately test BS and BI. Methodological aspects of all the studies will be discussed within the theoretical frame of the two-route model, as proposed by Dijkerman and de Haan (2007), and considerations on how to widen this model will also be discussed. This aspect has indeed been one of the aims of the work reported here (study 2).

Neuropsychological evidence: deafferentation and numb-sense.

Many different neuropsychological syndromes are explained as a consequence of a disruption of (at least one) body representation. The dichotomy Body Schema-Body Image is however grounded on a particular neurological syndrome: deafferentation (Brochier, Habib, and Brouchon 1994; P. Halligan et al. 2011; Paillard, Michel, and Stelmach 1983; Rossetti, Rode, and Boisson 1995). Deafferentation is a clinical condition characterized by a loss of somatosensory information that can affect a portion of the body. Central deafferentation arises after a lesion of the cortical/subcortical areas devoted to somatosensory processing, while peripheral deafferentation is a consequence of a lesion in the peripheral nerves. In both cases, body-parts localization in space, as well as appreciation of postural changes, are no more possible without constant visual control. Motor control and action execution might still be spared to different degrees, but heavily rely on visual feedback and sustained attention (Stenneken et al. 2006). Clearly, the lack of proprioception and the consequent deficit in motor control make deafferentation an interesting example of disruption of the Body Schema (de Vignemont 2010). An influential study by Paillard and colleagues (Paillard, Michel, and Stelmach 1983), reported a patient (RS) who, after a lesion following obstruction of the left posterior parietal artery, presented deficits for the right hand in joint position sense, as well as a in a single detection task and in the two point discrimination task[3]. The authors asked the blindfolded patient to point to tactile stimuli delivered in 18 different locations on the surface of her left (normal) or right (deafferented) hand. The main result was that, despite the fact that she was not able to feel the stimulation on the deafferented hand and to verbally report it, the patient could still localize tactile stimulation with a pointing movement of the other (spared) hand. Moreover, it is to notice that, even in absence of proprioception and with no visual control, the patient could still point with her right affected hand toward the healthy one, in order to localize the stimulations. These results suggest that a correct Body Schema was available for performing the motor task. Finally, as the authors pointed out, there was a difference in the error performance for the two hands: errors in localization on the deafferented hand were distributed in centripetal manner; while on the healthy hand they followed a centrifugal distribution. It thus seems that in absence of somatosensory feedback, the affected body-part is represented as shrunk[4].

It is important here to underline that the movement the patient was asked to perform was a ballistic pointing movement, which strengthen the unconscious sensorimotor aspect of the task. This type of movement relies indeed on fast action-related sensory information and does not necessarily involve more conscious perceptual processing of the stimulus. As already pointed out by Milner and Goodale (Milner and

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[3] The two-point discrimination is a spatial tactile threshold measurement that consists of delivering either one or two synchronous, but spatially separated tactile stimuli on the skin surface, varying the distance between them. In normal subjects, a threshold of a few millimeters is observable when the finger pad is tested. Larger threshold are observed when the same test is applied in regions of the body containing a lower density of mechanoreceptors with lager receptive fields (i.e., the arm or the calf).

[4] This observation seems to be in contrast with data about the perception of fingers size after digital nerve block (Gandevia and Phegan, 1999), that is a form of acute transient deafferentation. Body size knowledge and distortion in body representations will be discussed in the following paragraphs.

Goodale 2008b) in their revisited version of the two visual systems model, “The fact that a task involves action does not mean that the performance of this task would engage vision for action” (page 778). In particular, the authors suggested that the same motor task could involve processing of sensory information (visual in their case) in the perception stream when the task is perceptual in nature, but solved with a manual response. This issue had been anticipated, in the somatosensory domain, with another study on a deafferented patient (JA) by Rossetti and colleagues (Rossetti, Rode, and Boisson 1995; Rossetti, Rode, and Boisson 2001). JA suffered from a complete sensory loss of the right side of the body after a left parietal and thalamic lesion and, as the patient in Paillard and colleagues’ work, was unaware of any somatosensory stimulation despite a residual ability of localize them in particular conditions. In a first experiment, JA was asked to localize tactile stimuli delivered on the right hand through two different forced-choice tasks: a motor task (pointing with the left hand) or a verbal task (naming one of the previously shown possible site of stimulation). Patient’s performance was well above chance for the motor task (18 correct localizations out of 40 stimuli over 6 sites) while he was at chance level for the verbal task (4/21). Error distributions were also similar to those observed by Paillard, with a preferential direction toward the wrist suggesting that in absence of proprioception a shrinking of the hand representation occurs. The authors’ conclusion from the first experiment was that, even in absence of a conscious detection of the stimulation, localization was possible due to a spared low-level sensory-motor representation of the body configuration and position. However, they also pointed out that given the fact that in both cases forced-choice responses were asked, the dissociation showed by JA could not be ascribed to a conscious vs. unconscious processing of the information.

The novelty of the work by Rossetti and colleagues resides in addressing the question of whether the dissociation was to be ascribed to the output of the task (pointing vs. verbal response), or rather to the representation used to solve the task. In other words, the point here was to try disentangling between task and process. To answer this question they asked JA to localize the tactile stimulation delivered on the right hand through the same motor task, but toward a map of the arm and not his own body-part. The patient failed in performing the task suggesting that the tactile information could only be used to drive direct movement and not for higher-level processing. Despite using the same type of movement as in experiment 1, the fact that in experiment 2 the pointing movement was directed to a map and not the actual patient's body was sufficient to disrupt the residual abilities. This version of the task indeed requires a transformation from the localization on the skin to a conscious visual representation of the arm and, as a final step, the matching of this body-centered location and that based on an external map. This higher level processing was not possible in JA, probably because of the inability to store tactile and proprioceptive information long enough for such elaborate processing. This interpretation is supported by the results of an additional experiment, where the authors introduced three different delays between the tactile stimulation and the motor response. The shortest delay (1 s) had no effect on the patient's localization by pointing performance, which remained well above chance level, while the longer delays (2 and 4 s) produced a significant decrease in the patient's performance, which dropped to chance level. The conclusion of this last experiment was that the sensorimotor representation used for the ballistic pointing movement can not store information for more than one second, after which the information either accesses the higher level representation or, if this is not available, is lost. Interestingly, the authors also designed a proprioceptive version of this task where the experimenter positioned the patient's index finger either of two possible spots and the patient was asked to localize it through a pointing task. They found a pattern of results similar to the one with the tactile stimulation. However, a difference in the delayed condition was present. In particular, using three timings (0, 4 and 8 sec) the authors found that only in the 8-sec-delay condition the performance was disrupted (i.e. the ability to localize the deafferented finger was below chance level). This result suggests that the proprioceptive information can be retained for at least 4 sec, that is a much longer time than in the case of touch.

As a further step, Rossetti and colleagues also tested for the influence of perceptual processing on the motor response by asking JA to point to and name the location of the tactile stimuli at the same time. They found that performing the verbal task concurrently with the motor one destroyed the patient's spared ability to localize the stimulation with a motor action. This additional finding suggests a dominant role of the semantic on the sensorimotor system, at least in these conditions. Interestingly, the amplitude of the error in this dual task, that is the distance between the stimulated and located point, increased to values similar of those reported for the point-to-map task, suggesting that the motor task was performed using the same, perceptual, body representation. This result seems to fit a hierarchical organization of the somatosensory processing, whose higher levels are damaged in JA. The sensory information is thus available only for unconscious, relatively low-level processing subserving the ballistic pointing movement, but can not access higher level processes, necessary for verbal localization or spatial transformation from the body surface to the external space, as in the pointing to the map task. Moreover, the attempt to access this higher level processing has the consequence of destroying the relatively spared localization abilities.

The complementary dissociation has been reported by Cole and Paillard (1995) (see P. W. Halligan et al. 1995 for similar results). They described a peripherally deafferented patient (GL) who suffered from a selective loss of large myelinated fibers as a consequence of an acute viral infection. GL was able to perceive thermal stimuli on her skin, to verbally describe the location of the stimuli on her body surface and to show the same location on a map. However, when vision was prevented, she was unable to point directly to the stimulated body-part suggesting that she was unable to use her Body Schema simply by relying on proprioceptive information. To face her daily life problems she developed visual based strategies as a substitute of proprioception, even though these strategies had a huge attentional cost. For example, Cole and Paillard described how this patient learned to correctly shape her hand and control the grip force in order to grasp an egg, but that she could hold it only as long as her attention was not captured by a new event. Weight appreciation was also possible with visual control, with a good discrimination level (10 g in 150 g).

Gallagher and Cole (Gallagher and Cole 1998) reported a similar case (IW) who, similarly to GL, suffered from an acute neuropathy that caused the disruption of large fibers below the neck, leaving him with no proprioceptive information about the position of his limbs. Despite the pervasive disease, the patient had been able to recover important motor functions: he re-learned how to walk, to type on a keyboard, to perform movements under a constant visual and attentional control. The authors interpreted this behavior as evidencing the compensatory role of the Body Image, when the BS is lacking, also suggesting deep interconnections are present between the two body representations.

Finally, a recent study by Anema and coworkers (HA Anema, Zandvoort, et al. 2008) investigated the dissociation between BS and BI in two strokes patients (KE and JO) with intact basic somatosensory processing. Both patients were indeed able to perceive tactile stimuli delivered on their contralesional hand and arm, however their ability to localize the same stimulations varied depending on the task they were asked to perform. Above threshold stimulations were delivered on four different locations of the contralesional hand and patients were asked to point with the unstimulated (spared) hand either to the stimulated one, or to a map representing the stimulated hand. An additional task was used to control for basic motor abilities and consisted in pointing toward four visual targets. The two patients showed a different pattern of results, with KE being more impaired when asked to point to his hand, while JO performed better in the latter condition, but was impaired in the pointing to the map condition. Unfortunately, as discussed by the authors, the small number of trials recorded in each patient makes any further speculations difficult, in particular with respect to the spatial distribution of errors. In Paillard's work, the authors found a peculiar distribution of the final position of pointing movements toward the center of the hand, suggesting a deformation of the representation of the deafferented limb, mainly in the direction of a reduction in size. In Rossetti's work the same shift toward the wrist was present, supporting the notion of a shrinking in the hand representation in absence of proprioception. In Anema's paper the results follow the same trend. Patient KE seems to be selectively impaired in the distal-to-proximal direction when asked to point to his own hand, with a shift toward the wrist. However, visual inspection of the pointing performance (see Figure 8) suggests that, irrespective to the location of the tactile stimuli on the hand, all the movements were directed to the wrist, thus displaying a rather general bias (not a relative shift of each single stimulus) toward one region in body space. Moreover, in the task in which she showed a better performance (point-to-map), a general bias toward the left is observable, compatible with a hypermetric pointing performance. More strikingly, no spatial segregation is visible among landing positions to the four possible locations (the bottom-left spot is never correctly localized and there is a concentration of localization in the upper-left part of the hand; see figure 8).

Also JO exhibits a behavior compatible with a hyper-metric pointing performance in the unaffected task (point-to-hand), although a spatial segregation is still visible in this case.

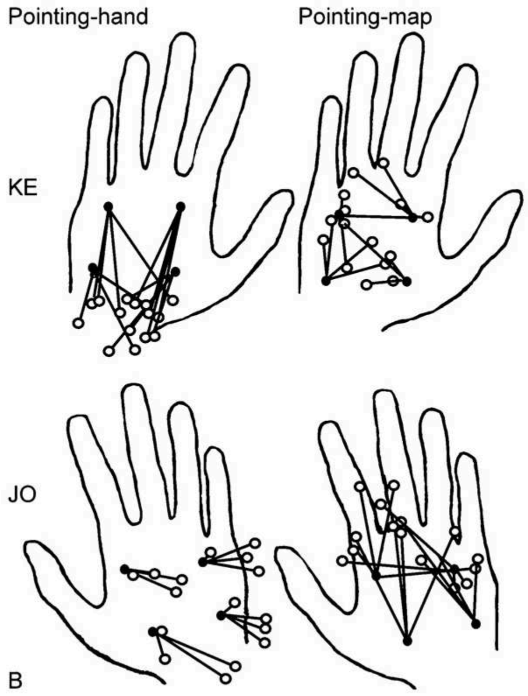

Figure 8. Pointing performance of patient KE (top) and JO (bottom) in the point-to-hand (left) and point-to-map (right) tasks.
From Anema et al, 2008

The case studies described in this paragraph allowed testing the three dimensions at the extremities of which the BS and the BI have been collocated (see table 1). The data discussed suggest that the strong dichotomy should be reconsidered as summarized in the following paragraphs.

Function

For the functional dimension, a dissociation between perception and action has been shown, supporting the idea that two separated representations are behind the two functions, namely the BS for action and the BI for perception. However, what is less clear is the relation between function and task. As already mentioned, Milner and Goodale (2008) pointed out, in the visual domain, that the fact that a subject is asked to make a movement doesn't imply that the same subject will process the sensory information in the dorsal, action pathway. Manual and arm responses have been used to perform perceptual judgments, as for example in size matching tasks, where subjects are asked to estimate the size of an object by opening the thumb and index finger (Westwood and Goodale 2003; H Anema, Wolswijk, et al. 2008). Similarly, in the body representation domain, movement performance can tap into the BI, as shown by Rossetti et al's work (2001), where with the same motor task they showed a dissociation between BS and BI.

The use of motor tasks to test the Body Schema is an important methodological and theoretical aspect. If we consider patient JA (Rossetti, Rode, and Boisson 1995) and GL (Cole and Paillard, 1995) and try to define their deficits on the basis of their ability to localize target via a pointing movement, one could say that they are both equally capable to do it and reach the (wrong) conclusion that their deficit is similar in nature. One would probably say that in both cases the BS is preserved, since movements are possible. However, this is not the case: JA is able to localize stimuli only through pointing movements directed to his own body, and not to a map of the body, while the opposite is true for GL. This suggests that a same output/response can rely on different body representation depending on the contextual task in which it is performed (Milner and Goodale, 2008; Kammers et al 2010) and implies that particular care has to be used in choosing the best methodological approach (this point will be more extensively discussed in the discussion of study 2).

Kammers and colleagues (MP Kammers, van der Ham, and Dijkerman 2006) applied the same rationale to a study on healthy subjects where they used a motor matching task to test the body representation for perception (this work will be extensively discussed in the following paragraph). I think the claim made by these authors about the need of a wider approach to the study of body representations is of great importance and, in line with Kammers and colleagues' recommendations (M Kammers, Mulder, et al. 2010), I used a multidimensional approach to assess the plasticity of the BS. In study 2 (see results section), two different outputs (motor or perceptual) were coupled with two possible inputs (tactile or verbal) to investigate (1) the possibility to accessing the BS plasticity and (2) to test, in healthy subjects, the selective effects of tool-use on the body representation for action.

Consciousness

The second dimension along which BS and BI are classified is consciousness. BS has been classically considered as an unconscious representation that does not need awareness to be updated. Paillard and coworkers (1983) reported that their patient was completely unaware of the tactile stimulation received and surprised by her ability to point to it (*"I don't understand! You put something here. I don't feel anything and yet I go there with my finger. How does that happen?"* p. 550). Despite this inability to perceive it, the very same tactile stimulation that could not reach consciousness was processed inside the BS, mapped on a represented arm position and allowed a correct localization through a pointing movement.

Rossetti and colleagues (1995, 2001) suggested that hierarchical organization exists, where the conscious processing acts as a higher-level controller of the unconscious system, as shown by the disruption of the spared localization abilities in JA when the pointing movement was simultaneously performed with a verbal (conscious) task. These results suggest the BS is an unconscious representation; however, as recalled at the beginning of this paragraph, this does not mean that we cannot be aware of the position (and size) of our body-parts. Instead, as Head and Holmes wrote in their paper (1911-12), it means that the update occurs under the level of consciousness, but the result can reach consciousness, and so can be verbalized and consciously elaborated, as in the case of motor imagery tasks. The BI, as it is conceived in dyadic models, is conscious and it is indeed involved in perceptual tasks, or better processes, where the body information is consciously processed (verbal localization, non ballistic pointing movements). Therefore, along this dimension, we can't readily place BS and BI at the two extremities and so we can't strictly talk about dissociation. However, we can dissociate between the level of consciousness required to access a body representation and that required to process information and build the body representation. As mentioned above, it is the updating of the BS that is unconscious while we can verbally (i.e. consciously) report a change in body configuration. This has two important implications. The first is, again, the need of a wider and more articulated experimental approach that takes into account the possible dissociation between unconscious processing vs. conscious report. The second, a direct consequence of the first implication, is the importance of studying both body representations in dynamic situations by inducing plastic changes (see study 2).

Temporal dynamic

Finally, the third dimension is the temporal dynamics. Rossetti et al (2001) investigated the temporal aspect by introducing a temporal delay between the stimulation and the localization pointing. They found that the representation that guides action could store the information for about 1 to 4 seconds, depending on the sensory modality (touch or proprioception). Moreover, we saw (Rossetti et al, 1995; see study 2 in this thesis for similar results) that only ballistic fast movements are guided by the BS. These results suggest that the BS is a short-term representation where the actual state of the body is stored for a very short time and constantly updated to efficiently serve action performance. However, some of the action-relevant information about the body are more constant than other. Position in space changes more often and quickly than body-parts' size, although both are fundamental for performing actions. As de Vignemont (2010) suggested, it is unlikely that the BS re-calculate body-parts' size each time we move, as it would be indeed too costly. At the same time, growth is not the only source of changes in body size. Tools can, and are often used to, overcome body limitations producing an abrupt increase in size. This would imply that in some way the BS should be able to quickly recognize when effectors' size has to be recalculated (see study 1), possibly being able to even make the difference between a size change induced by tool-use or by a body lengthening (see study 3). In conclusion, along the temporal axis, BS cannot be placed to one of the extremities, as both long-term and short-term bodily information are used.

	Body Schema	Body Image
Function	Action	Perception
Consciousness	Unconscious Update	Conscious
Temporal dynamics	Short-term (position and size) Long-term (size and shape)	Long-term

Before critically reviewing the studies on healthy subjects, I would like to discuss two main problematic issues about the definition of BI and BS. The first concerns the spatial boundary of these representations, the second concerns the ownerships of each representation's content.

The former point lies in the following sentence in Gallagher and Cole's paper (1995):

"Body image boundaries tend to be relatively clearly defined. The body schema, in contrast, can be functionally integrated with its environment, even to the extent that it frequently incorporates certain objects into its operations--the hammer in the carpenter's hand, the feather in the woman's hat, and so forth".

A growing part of the literature has shown that Body Image boundaries are far from being sharp. In this respect, the Rubber Hand Illusion (RHI) (Botvinick & Cohen, 1998) is probably the most striking example of the brain's capacity to integrate inanimate objects on the perceptual representation of the body (For its importance in the study of body representations in healthy subjects, the illusion will be illustrated in the following paragraph). When considering instead the extent of the Body Schema, we showed that it is a highly plastic representation (Cardinali et al. 2009; Cardinali et al. 2011), however we will also show that there are limits to the Body Schema plasticity that are mainly related to objects that participates to action performance (and it's not really the case for the *feather in the woman's hat*, no matter how charming the example is). A recent study by Newport and colleagues (Newport, Pearce, and Preston 2010) also showed that the possibility to incorporate external objects, like fake duplicates of the subject's hands, can overcome plausibility rules for the BI, but not for the BS. Using a modified version of the RHI paradigm, they induced in healthy subjects the illusion of having two supplemental hands (and not just one as in the classical version of the RHI). They showed that the BI was sensitive to this illusion as the subjects reported feeling of ownership for both supernumerary hands, but the BS resisted the illusion, allowing the incorporation of only one hand (this study will be more extensively explained and discussed in the following paragraph).

The second issue deserving discussion is about the description of the Body Image as *my own* body, while the Body Schema would be a rather "anonymous process" (Gallagher and Cole, 1995). I wish to suggest here that there might be a confound in this respect, possibly arising from the conscious-unconscious nature of the two representations. The BS is built mainly on the basis of proprioceptive information, which is the most body-related sensation, in the sense that it informs the brain about the state of *my* body -not *a* body- and it is used to plan and implement actions on my body, again not a body. It seems thus difficult to refer to the BS as an anonymous and pre-personal representation, unless one does not use consciousness to define what is personal.

A recently advanced bodily-self theory (Gallese & Sinigaglia, 2010) posits that the sense of self does not exist outside the body, but it is rather a sense of body that is enactive in nature and is to be found in the power of action. In other words, it identifies the self in the action potentiality of the body. It seems then that, at least according to this model, the Body Schema can not be considered of as an impersonal representation, but rather as the source of the self itself. At the same time, since early in life, we are able to imitate observed behaviors. Many studies showed that newborn are able to reproduce face movements when they see them in an adult (Meltzoff and Moore, 1977). At the basis of this capacity lies the ability of matching *my* face's movements with those of *your* face. This seems to suggest that the BS can not be described as strictly personal, nor strictly un-personal. However, in a recently proposed theory of the origin of the sense of ownership (de Vignemont 2007), de Vignemont describes the BS as a self-specific representation of the body that is not shared between the self and the other and, of particular relevance for this thesis, represents the acting body. As such, the BS becomes the source of the sense of ownership as it constitutes the spatial content of the bodily sensations.

I think that the personal/un-personal nature of the BS is an important issue, in particular when addressed in the context of mirror neuron mechanism theories.

The mirror mechanism consists of a peculiar activity of certain neurons that are activated both when an individual performs an action and when observes someone else performing the same action. Since their first discovery in the macaque brain area F5 (di Pellegrino et al. 1992) many researches have been conducted to elucidate the characteristics and functions of mirror neurons. In the macaque brain three major brain areas have been described as the mirror circuit of grasping: a frontal area (F5a, p and c), a parietal area (AIP and PFG) and a temporal area (STS).

A growing amount of functional neuroimaging literature supports the notion that in the human brain mirror neurons/systems exist, in particular in the inferior precentral gyrus, inferior frontal gyrus and the inferior parietal lobule, although the first electrophysiological recordings of mirror neurons activity has been documented in other areas (Mukamel et al. 2010). It has been proposed that the mirror mechanism play a crucial role in action understanding since it allows a complete matching between the sensory (visual or auditory) experience of someone else's action and one's own motor experience (Rizzolatti and Sinigaglia 2010).

The specificity of the mirror neurons of the human brain is that they are able to code the goal (i.e. firing according to the aim of the observed movement, independently from the effector used to achieve it), as in monkeys (Umiltà et al. 2008), but also single-movements (Gazzola and Keysers 2009; Cattaneo et al. 2009). The discovery of this mechanism, as well as the observation of early imitative behavior in newborn, challenge the idea of a BS as personal representation. However, as we will see in study 3, this representation seems to be particularly sensitive to the way it is updated, so possibly to the motor potentiality.

Evidence from healthy subjects

Only recently, dissociations have been provided in healthy subjects supporting the existence and relative independence of Body Schema and Body Image. All these studies used different types of sensory illusions, and particularly the tendon vibration (Kammers, van der Ham, and Dijkerman 2006) and the RHI (Tsakiris and Haggard 2005; Kammers et al. 2009; Kammers et al. 2010) which was already mentioned in the former paragraph and will be explained in more details below.

When a vibration at a frequency of 75 Hz is applied on the sinew of an immobilized limb muscle, an illusory extension of the muscle length is produced that leads to the experience of an illusionary movement of the limb. Kammers and colleagues (2006) used this illusion to dissociate BS and BI by asking subjects to perform three different localization tasks. Two illusion conditions were used while subjects were asked to localize body-parts with different tasks (see below). In the “direct” condition, the vibration was applied to the biceps brachii tendon of the right dominant arm and subjects were asked to localize the arm; the “indirect” condition, where the same vibration was applied to the same muscle while subjects were holding the right knee and asked to localize the knee. In this way, the authors have been able to vary the level of competition between sensory input informing the brain about a (unreal) displacement of the limb, i.e. the signals coming from the muscle spindles provoked by the vibration, and the other information coming from the skin and other tendon receptors about the fact that the limb actually didn’t move. The direct condition maximized the first type of inputs, whereas in the indirect condition the amount of information increased, i.e., that coming from the knee joints and skin, was ‘against’ the presence of a movement. To separately test either body representation, subjects were asked to localize the right arm with three different tasks: a ‘perceptual’ task, consisting of an active matching of the right (vibrated) arm position with the left (un-stimulated) arm and a motor task, consisting of a reach-to-point movement of the left hand toward the right one, were used in the Experiment 1. In Experiment 2 the authors added a passive matching task where the left (un-stimulated) arm was passively moved by the experimenter and subjects had to stop the movement when they thought the left arm matched the right (stimulated) one in position.

Owing to the definition of the BS as a proprioceptively based representation of the body, one would expect the motor task to be more influenced by this kinaesthetic illusion than the BI. However, results showed that the two matching tasks were much more affected (in both direct and indirect conditions) than the motor one. Moreover, a difference was present also between the two former conditions; the subjects showing a larger perceived displacement in the "direct" one (when asked to directly locate the vibrated arm). A significant interaction was present between condition and task, showing that the matching in the direct condition was significantly more affected than that observed in the other tasks. These results are somewhat puzzling. In the introduction, the authors predicted the effect of the kinaesthetic illusion on the BI in the following way: *"Body Image may use stored knowledge from experience that stretching of the biceps is caused by lowering the arm, to override the conflicting information and in this way minimize uncertainty"* (p. 2431) while the BS should resist to the illusion *"since there might be more proprioceptive input suggesting that the arm is stationary, instead of moving"*. In other words, they suggest that the BS is more heavily based on proprioceptive information, but at the same time is not affected by a massive event as the perceived movement of a limb[5]. However, the BI that is mainly a visually-based body representation, was strongly affected, with subjects showing an arm drift of about 6 cm. Some methodological issues are discussed by the authors. First of all, in the first experiment, when pointing to the vibrated arm, subjects were allowed to touch the body-part, which provides an important feedback to correct the subsequent movements. Moreover, the performance was not corrected for a baseline, which was not performed meaning that the drift showed in the Experiment 1 was not corrected for a general shift in proprioception independent from the induced vibration (Wann and Ibrahim 1992). Interestingly, when the baseline has been introduced in Experiment 2, the amount of the drift recorded with both matching tasks was reduced by half of its amplitude. Surprisingly, in this second experiment, where tactile feedback was prevented by a plastic sheet, subjects performed even better than in the previous experiment, although one would not expect to find an improvement in the performance when no feedback is provided.

Recently, converging results supporting dyadic models of body representation have been provided by experimenters using the RHI (Botvinick and Cohen 1998;

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[5] Unfortunately, in the second experiment authors compared the three tasks among them but not each of them with 0, meaning that it is not possible to know if the deviant score of the motor response is significantly bigger than 0

Kammers, Kootker, et al. 2010; Tsakiris et al. 2010). In this famous and widely used illusion, subjects experience a sense of ownership of a fake hand, placed in a plausible posture, after synchronous stimulation of their own (unseen) hand and the visible fake one. In a classical setup, subjects are seated in front of a table where their hand, hidden from sight, is placed close to a visible rubber hand. They are instructed to look at the fake hand while the experimenter brushes both hands in an asynchronous or synchronous fashion (i.e. introducing or not a temporal delay between the touch on the two hands and, as a consequence, between the visual and the tactile information). In the synchronous condition, the conflict among the location of the seen touched hand, the perceived touch and the proprioceptively located hand is solved by the brain assuming that what is felt is where it is seen. In other words, the conflict is solved in favor of the visual information, with a recalibration of the proprioceptive information that results in the feeling that the position of the real hand is shifted toward the position of the rubber hand. Indeed, the incorporation of the rubber hand is typically tested through two indexes: the proprioceptive drift, that is the shift in the perception of the position of the hand under illusion, and the personal report of the subjects, as measured with ad hoc questionnaires.

For the RHI to occur four conditions seem to be essential. The first one is the synchrony between the stroking of the two hands. The illusion indeed arises only when the seen and perceived touches happen at the same time. The second is the spatial compatibility between the position of the real and the rubber hand. Tsakiris and Haggard (2005) tested a group of subjects in a RHI setup in two different conditions, one in which the rubber hand was aligned with the real one and another where the rubber hand was tilted of 90° in respect to the real one. They found that only the condition in which the rubber and real hand were aligned was effective in eliciting a positive proprioceptive drift, which is a perceived shift in the position of the real hand toward the rubber hand. In the same study, the authors tested also for the possibility to induce the same type of illusion when stroking a neutral object. If the illusion is simply the result of a bottom-up association between vision and touch, stroking a wooden stick should be sufficient to induce the illusion. This doesn't seem to be the case, as they did not found any significant drift when the tactile stimulation on the subject's hand was synchronously delivered with a same stimulation on a wooden stick. (see Tsakiris et al 2010 for similar results). Similarly, the authors did not succeed in inducing the illusion when the laterality of the rubber hand was not congruent with the real one, thus strengthening the hypothesis that RHI is not the result of a purely bottom-up association. Finally, the shift in the proprioceptively perceived position seems to be a local phenomenon that concerns only the stimulated finger and not an adjacent, non-stimulated finger. When both the subjects' and rubber hands were stimulated on the index finger, the authors found a drift only when the finger to be subsequently localized was the one stimulated (index) during the induction of the illusion, and not the little finger. This result suggests that the drift concerns only the stimulated finger and not the entire hand. However, when two fingers (index and little) are stimulated and subjects are asked to localize a third one (the middle finger) whose position is in between the two stimulated ones, the drift is present also for this finger. This clearly shows a top-down modulation of the illusion and in particular the involvement of a representation of the hand that specifies the relative position of the fingers. Together with the drift of the perceived position of the stimulated real hand, subjects also experience a sense of ownership of the fake hand, as measured by questionnaire. Also this subjective feeling of ownership is present only when the above conditions are satisfied. Altogether, these findings suggest that the bottom-up coupling between visual and tactile stimulation is a necessary condition to evoke such an illusion, but is however not sufficient, as the illusion is clearly modulated by top-down mechanisms, and in particular by the representation of the body (Costantini and Haggard 2007). When the rules of this body representation are violated, as in the case of an incompatible posture of the rubber hand or an incongruence of the fake hand laterality, the illusion is broken.

The richness of the RHI paradigm in terms of the number of questions that can be addressed through it, together with the easiness with which the illusion can be elicited, have made of the RHI one of the most popular experimental approaches to the study of body representations. One of the main questions that have been addressed is whether the rubber hand is incorporated in the Body Image or in the Body Schema, or in both. Similarly to what has been done in patients studies, this hypothesis has been tested following the two routes model, by designing motor and perceptual tasks to test the proprioceptive drift and look for a potential dissociation between BS and BI. The rationale behind these studies is that, if the rubber hand is integrated in the BI, then perceptual localization tasks should be affected by the illusion and motor tasks would not, and vice versa, if the incorporation happens to occur at the level of the Body Schema.

Kammers and colleagues (2009) tested a group of healthy subjects with a classical RHI paradigm. In a first experiment they use an articulated experimental design where, after 90s of synchronous or asynchronous stimulation of the subjects' right index finger and the equivalent finger of the rubber hand, a first perceptual response was recorded about the position of the stimulated finger. Subjects saw the experimenter moving her own finger on a board placed above the table were the three hands were placed (the right and left subject's hands and the right rubber hand). They were asked to stop the experimenter when they estimated that her finger was in a location that corresponded to the position of their own right (or left, according to the condition) index finger. This first perceptual response was followed by a first motor response, which consisted in a ballistic pointing to localize either the right or the left hand, using respectively the left or the right hand. A second motor response was then required, by using either the same or a different hand with respect to the one used in the previous trial. Finally, a second perceptual task, identical to the first one, was performed. This particular paradigm allowed the authors to compare motor and perceptual tasks and to see whether the RHI could affect the BI (as a change in the perceptual localization task would suggest) and/or the BS (as a change in the pointing kinematics would testify). Moreover, the second perceptual task was designed to establish the effect possibly caused by the arrival of fresh proprioceptive and kinesthetic inputs from the motor task on the persistence of the RHI. In other words, perceptual retesting was meant to assess the strength of the illusion against new somatosensory information. In a second experiment of the same study, the perceptual task consisted in verbally choosing among three sticks the one that matched the distance between the subjects' hands, whereas the motor task consisted in picking it up with a bimanual fast grasping movement. Similarly to previous studies (Ehrsson 2004; Ehrsson 2005) the authors found that the perceptual tasks were sensitive to the illusion. When asked to judge the position of their right index finger by verbally positioning the experimenter's fingers (exp.1) or choosing a stick (exp.2), subjects showed a larger drift (about 6 cm) toward the rubber hand for the synchronous, compared to the asynchronous condition. In other words, their perceptual localization of the stimulated hand was incorrect. However, when the localization of the right index finger was assessed through a motor task and in particular with a ballistic pointing, the authors observed no significant drift. Moreover, when the stimulated hand was used to point to the left one, the kinematic profile was not affected, as one would predict if the representation of the hand position used to point was resistent to the illusion. This suggests that the same hand that is localized perceptually as being displaced in space is perfectly well located when a motor task is required.

These findings strongly support the idea that two different body representations are used for motor and perceptual tasks. These two representations, the BS and the BI, are characterized by a different weighting of the sensory information: the BI is more influenced by visual information, as shown by the visual dominance on touch and proprioception that is the base of the RHI; on the contrary, the BS is mainly based on proprioceptive information, which is more relevant for a correct (pointing) action execution.

Another important result from the above reported study emerges from the second perceptual task, performed after the two pointing movements. After reaching twice with the left hand, that is when no new afferent information were provided to the (right) stimulated hand, the strength of the illusion is unaffected: subjects still judged their right hand to lay about 6 cm toward the rubber hand. However, when the (right) stimulated hand was used to perform one of the motor responses, the newly provided kinestesic and proprioceptive inputs were capable of reducing the proprioceptive drift, by about half of its original amplitude, and this was even more pronounced when the right hand was used for both pointing movements. However, this is only a partial reduction of the drift, which remains significantly larger when compared to the control asynchronous condition. This suggest that the two representations subserving the two tasks are separated, but nevertheless interact and that the main difference between them might arise from the weight that is attributed to visual and proprioceptive inputs in the updating processes.

In a subsequent study, the same group showed that when the emphasis is placed on the action performance, the RHI can indeed affect the BS (Kammers et al, 2010). In this new version of the illusion, subjects kept their right stimulated hand (unseen) in a grasping posture, that is with the little finger resting on the table and the thumb and the other fingers open in a grasp position. The rubber hand was placed above the real one in a similar posture, but with either a smaller or a bigger finger grip aperture. The authors found an effect on subsequent grasping movements, and in particular that the maximal grip aperture was influenced by the size of the rubber hand grip aperture. When asked to grasp a same object, subjects opened their thumb and index finger wider when they experienced the illusion of owning a RH with a larger grip aperture. The peak of velocity of the movement was also modulated by the type of rubber hand used to induce the illusion.

This study suggests that, at least in certain conditions, the BS can be sensitive to the RHI. The first main difference with the previous study is in the posture of the hands, which strengthen the motoric aspect. This is supported by a recent work by Gentilucci and colleagues (Gentilucci and Campione 2011) who revealed in a series of elegant studies that the posture assumed by an effector can have an influence even on the kinematic of a different effector. Second, the tactile stimulation provided during the induction phase involved both thumb and index finger. As already discussed in this paragraph, Tsakiris and Haggard (2005) showed that the RHI, when induced passively without any sense of agency[6], is a local phenomenon and results in a change in the perception of the hand position that is limited to the passively stimulated finger, but does not affect the adjacent one. This result led to a definition of the BI as a fragmented representation, in opposition to a more holistic BS. By using this particular grasping posture and/or stimulating both the index and thumb fingers, the authors created the ideal conditions to have a whole hand illusion. It is to notice that in this particular posture, the index finger is directly in contact with the middle, which is touching the ring finger and so on. It might be argued that this particular configuration of the hand with the index finger touching the others would

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[6] The sense of agency is defined as the feeling to be the initiator and controller of an action (Jeannerod, 2003). By definition, passive movements do not involve agency as they are not initiated nor controlled by the subject.

more likely produce a drift in the perception of the other three fingers because of the contiguity and because of the necessity of keeping a coherence between the newly felt position of the index finger and the tactile information about the index finger being in contact with the middle. It has been indeed shown that a change in the perception of the position of a body segment can induce a change in perception of position/size of another body-part that is in contact with the first one. Lackner (Lackner, 1988) vibrated alternatively the biceps brachii (uni or bilaterally), or the antagonist muscles of healthy blindfolded subjects. The vibration produced an illusionary sensation of movement of the vibrated body-part, the arm. He also asked subjects to hold different body-parts (the nose, the buttock or the head) during the vibration period and then to report the experienced sensations. He found that, depending on the direction of the induced illusionary displacement of the arm, subject could feel the held (unstimulated) body-part changing in size. One could advance that the BS, which is informed about the arm displacement, tries to keep a coherent representation of the position of both the arm and the body-part held by it. The tactile information about the contact between the vibrated arm and hand and the nose, for example, is coupled with the proprioceptive inputs about the illusionary displacement and results in what is known as the Pinocchio Illusion, which is a feeling of the nose increasing in length. Interestingly, this illusion has been more recently shown to be able to influence subjects' estimation of tactile length (de Vignemont, Ehrsson, & Haggard, 2005). Subjects perceive tactile stimulation applied on the body-part that is felt being longer, because of the illusion, are estimated as further apart from each other, when compared to a baseline condition when no illusion is present. As we saw in the previous reported experiments, this perceptual task is supposed to involve the BI while the proprioceptively driven illusion is more likely due to a change in the BS. This result thus suggests again an interaction between the two representations and/or a dynamic recruitment of one or the other body representation, depending on the type of task required and/or the weight accorded to the current sensory information.

In a similar study using the RHI illusion, Newport and colleagues (2010) have been able to report effects on motor responses after the illusion induction. The particularity of this study comes from the fact that subjects have been presented with two images of their own left hand, shifted on the right and on the left of the real unseen left hand. Moreover, an active touch was used to induce the illusion. Subjects were asked to stroke the bristles of a toothbrush, for only 20s while watching one or two hands duplicate that were visually acting synchronously or asynchronously with the actual tactile stimulation. Two different stimulation conditions were designed: a unilateral condition, in which only one duplicate hand, either the leftward- or the rightward-shifted, was synchronously moving with the real hand; a bilateral condition, in which both fake hands were moving synchronously with the real one. Both motor and perceptual tasks were administered after the illusion induction. The perceptual task consisted of a questionnaire about the conscious perceptual experience of the illusion, while the motor task consisted of performing three subsequent pointing movements toward a visual target. When comparing the synchronous versus the asynchronous condition, the authors found a significant effect in the responses to the questionnaire for both conditions (uni- and bilateral) only in the synchronous condition, suggesting that the BI is able to incorporate not only one, but two images of fake hands with an active stroking task. Interestingly, the results of the motor task for the unilateral condition showed that the incorporation in the BI was accompanied by a modification of the BS. The final error point was indeed affected by the condition, with a rightward shift in the reached end points when the incorporated fake hand was the one on the left, and a leftward deviation of the end points when the fake right hand was incorporated. The authors thus suggested that a modification of the motoric body representation is observable when the illusion is induced using an active movement. These data seems to be in contrast with one of the Kammers and colleagues' study in which the authors failed to report an effect of the RHI on motor pointing. However, the difference in the induction of the illusion could be the key to understand this difference. Newport et al's used an active version of the task where the tactile stimulation was a consequence of the action performed by the subjects. This type of protocol strengthens the motoric aspect of the task and gives another value to the received tactile input. In the active stroking, the tactile input is not a simple external event, but the expected consequence of an action. We know, indeed, that the brain anticipates the perceptual consequences of an action (Miall and Wolpert 1996). The congruency between the expected perceptual outcome and the actual tactile consequences of the performed action can play a crucial role in strengthening the idea that the finger the subject is moving is the one that is seen moving. Moreover, with this particular paradigm the subject experiences also a sense of agency for the action seen. In addition, this interpretation is compatible with the more recent work by Kammers and colleagues (2010) where the authors showed an effect on kinematics of grasping movements after RHI, provided it is elicited on the whole hand.

Most interestingly, Newport et al's further found that in the bilateral condition, when both duplicate hands were moving synchronously with the real hand, the subsequent motor response were significantly deviated to the left, as in the unilateral right condition. This finding suggests that only one hand was controlled and incorporated in the BS, even though the perceptual task in the same condition suggested an incorporation of both hands into the BI. Interestingly, this paradigm allowed the authors to underline a difference between the two representations in terms of possible incorporation of supernumerary limbs. The Body Image seems to be able to incorporate at least two additional hands (see also Guterstam, Petkova, and Ehrsson 2011), while the Body Schema can control only one at a time. Giving the fact that having a supernumerary limb is a violation of the normal human body structure, what could make the BI accepting such a situation as possible? And what could make the BS be instead reluctant to this same possibility? One could argue the difference may lay in the plausibility of the situation. In particular, it is plausible and common experience to receive tactile input through objects that are not our own body-parts (although they are in contact with them). Yamamoto and Kitazawa showed, for example, that we can feel a tactile stimulation delivered to the tip of a drum stick (Yamamoto and Kitazawa 2001). Tactile sensations can come at the same time from our own body (the hand in this case) and the tip of the tool so that we can receive different sensory information from different extremities at the same time. However, we cannot send motor commands to other extremities but our own arms. Of course, we can control tools with our hands, but the motor command is sent to our muscles that indirectly produce the movement of the tool. This suggests that the limits of the plasticity of the BS may be dictated by the action possibility, that is the possibility to implement, or not, an action on the effector.

Interestingly, in the condition where two hands were synchronously moving, all the subjects but one showed a reaching trajectory that was compatible with an incorporation of the rightward duplicate of the subject's hand. It is to notice that that hand is the one closer to the midline. It has been previously reported that proprioception of upper limb can drift toward the midline when vision is occluded (Wann and Ibrahim, 1992). Although in the baseline condition Newport and colleagues did not find any drift, it is possible to hypothesize that in case of such a conflicting situation where two hands are present and both move synchronously with the real one, as the one of the two fake hands, the potential conflict is solved in the direction of this bias toward the midline that seems to be present in the proprioceptive system.

To summarize, the literature offers a consistent body of evidence that supports the existence of two separated body representations: these have been referred to as the BS and BI by most of the studies reported above, which frame the body representational problem in dyadic models. There is quite large consensus that the Body Schema is an action devoted schema of body-parts (size) and position in space and therefore tested with motor tasks. It is also largely acknowledged that the BS is an unconscious representation that is updated at every movement and allows appreciating postural changes and performing motor control accurately. Proprioception seems to be the key sensory information used for updating the BS and its disruption leads to deficits in the ability to correctly localize and act on the body surface. It is a holistic representation, where internal coherence is maintained and supposed to be highly plastic. Pretty much on the opposite side, the Body Image has been described as a perceptual representation of the body subserving identification of stimulated body-parts. It is a conscious representation and can accept inconsistency as for example the ownership of supernumerary limbs. The two representations differ also in term of temporal dynamics, although we already have seen in the previous paragraph the BS and BI cannot be placed at the two extremities of this axis (see page 32).

Triadic and Tetrad models

Triadic models essentially respond to the need of a clearer description of the Body Image. In the previous paragraph we referred to the BI as a perceptual, conscious, long term representation of the body, mainly tested with perceptual localization tasks. However, in the literature, disparate descriptions have been proposed that made difficult a sharable and, most important, operational definition of this particular representation. Gallagher and Cole (1995), for example, wrote that:

"The body image consists of a complex set of intentional states--perceptions, mental representations, beliefs, and attitudes--in which the intentional object of such states is one's own body. Thus the body image involves a reflective intentionality. Three modalities of this reflective intentionality are often distinguished: (a) the subject's perceptual experience of his/her own body; (b) the subject's conceptual understanding (including mythical and/or scientific knowledge) of the body in general; and (c) the subject's emotional attitude toward his/her own body".

In this description, many levels of the body knowledge and experience are pooled under one single label as if they were supported by the same body representation. At the same time, neuropsychological studies showed that a cortical lesion can produce an impairment of one aspect of this body knowledge, while leaving the others intact.

Sirigu and colleagues (Sirigu et al. 1991) tested D.L.S., a 62-yr-old patient affected by an early form of Alzheimer disease, by using different body-part localization tasks. Pointing tasks were triggered either by verbal instructions ("point to the knee") or visual cues ("touch on your body the body-part the experimenter is touching on himself"). Two naming tasks were also used where the patient had to name body-parts indicated by the examiner on the patient's body, or on the examiner's body. In this way, the authors could test the ability of the patient to localize body-parts on her own body, the experimenter's body or a doll's body. As a control for the integrity of basic pointing movements and for excluding a problem in the analysis of complex stimuli, they also asked the patient to point to parts of inanimate objects. Despite a perfect performance was observed in the latter task, the patient was unable to point to any body-part on her own body, as well as on the experimenter's or the doll's body, either after verbal and visual command. A qualitative analysis of the pointing movements revealed a prevalence of contiguity mislocalizations (pointing to body-parts close to the target one), such as the lower arm for the elbow, followed by functional errors (pointing to a body-part similar in function, such as the knee for the elbow). However, the patient was able to name body-parts shown on her or the experimenter's body, as she was able to describe their function, but not to describe their position. The specificity of this problem for body-parts is also shown by the fact that, when pictures where attached to the same body-parts she was unable to localize, pointing movements directed to those pictures were accurate. This series of studies clearly shows that a spatial representation of the body structure exists and that it is damaged in D.L.S. Less clear is the model of body representations proposed by the authors to explain the disorder. Sirigu and colleagues proposed the existence of (at least!) four body representations (p.637). The first is the Semantic and lexical representation and, as the name says, contains the semantic knowledge of body-parts. It is responsible of the ability of naming body-parts, to describe the functional relationship that exists among them, as well as their function. It is described as being propositional in nature and tightly linked to the verbal system. This representation is not affected in D.L.S., given her ability to answer correctly to questions such as "what is the mouth for?" or "what are the hands for?". A second representation (Structural Description of the Body) is supposed to contain a visuo-spatial scheme of the human body (although animal's body have not been used as control in this study). It describes the structure of the body, specifying the proximity relationship existing between body-parts and their boundaries. It is described as being linked to non verbal, visual and somatosensory systems. The third level is the "emergent body-reference system" that is a representation of position in space of the different body-parts, it provides information about the movements of the body-parts in the external space and in respect to one another. It is described as being built on multisensory information and, despite the use of the term "body image" in its description, it appears to better correspond to the Body Schema, as it has been described in the previous paragraphs. Finally, the fourth level consists of a motor representation, not further described, which corresponds more to a set of motor commands and movements than to a body representational level. Sirigu and colleagues' model of body representations has indeed been cited since afterward as a triadic model. As one can easily understand, this model maintains the existence of a Body Schema, but splits the vague concept of Body Image in two different representations: one semantic and the other spatial.

The validity of this model has been more recently tested by Schwoebel and Coslett (Schwoebel and Coslett 2005) in what is the only study, so far, on a large group of brain damaged patients. The authors tested 70 stroke patients by using a battery of tasks designed to test the three body representations proposed in Sirigu and colleagues' work. The rationale behind this study was that tasks designed to assess a particular body representation should be strongly correlated among them, while a low correlation should be found between tasks designed to test different representations. For testing the BS they used a motor imagery task where patients were asked to imagine performing four different movements with the ipsilesional and contralesional hand, in separated sessions. A ratio between the movement time needed for the imagery task and its actual execution was calculated for each movement. The second task was the hand laterality task: patients had to judge the laterality of a seen line-drawing of a hand, presented with either a palm-up or a palm-down position and in one of 4 different orientations (with fingers pointing to the left, right, away or toward the patient's body). Owing to the definition of the BS as a motor devoted representation, one could argue that these two tasks do not involve a movement and so they can not be sensible to BS disruption. However, it has been shown that motor imagery engages the BS, as well as actual movements (Cooper and Shepard 1975; Parsons 1987). Cooper and Shepard (1975) showed that when asked to judge whether a seen hand is a left or a right one, subjects solve this task by mentally rotating their own hand until it matches the seen one. Moreover, the reaction time depends strongly on the amplitude of the movement that has to be imagined to solve the task and correlates with the time needed to actually perform that movement (Parsons, 1987). In other words, solving the hand laterality task is based on motor imagery of one's own body, which is influenced by the actual representation of the body position in space, i.e., by the BS.

For testing the Body Structural Description (BSD) the authors used localization tasks of either a body-part or tactile stimulation, and a matching of body-parts by location. Both localization tasks consisted of pointing with non-ballistic movements: the first one consisted in pointing to one's own body-part that corresponded to the one shown in a picture. In the second task, subjects were asked to indicate on a map where they had been touched. It is to notice that this last test is the same as the one used in previous studies (Paillard et al 1983; Rossetti et al, 1995, 2000, Anema et al 2009) to investigate the BI. Finally, the matching task consisted of choosing among 3 pictures the one that represented a body-part spatially close to the target one that was shown on a picture.

The BI was here tested with two matching tasks that involved a functional knowledge about the body. The same pictures as those used in the matching task for the BSD were presented to the participants who had to pair them based on functional similarities (for example, the elbow and the knee, as they both are articulations), or to the associated clothes/objects (wrist and watch, foot and shoe, etc.).

Schwoebel and Coslett ran a principal component analysis on the patient's data and found indeed a high correlation between the scores for the tasks aimed at testing for the body image. Similarly, they also found a correlation between those tasks aimed at testing for the body structural description but not between the tasks for the body image and those for the body structural description, supporting the idea that those two representations are separated and can be selectively damaged following brain lesion. Interestingly, the two tasks designed for the BS, the motor imagery and the hand laterality, did not correlate. The authors suggested two possible explanations. The first one concerns the fact that the two tasks differ in term of explicit/implicit processing of the body position in space. The hand laterality requires indeed an implicit processing of subjects' hand posture, while the motor imagery task involves an explicit movement simulation. A second proposed difference resides in the fact that the laterality task is solved with a rotation of the entire arm while the motor imagery implies imaging movements of the single hand or specific fingers. Despite this dissociation, both tasks showed a bilateral effect: patients' performances were affected, no matter which hand was used. More importantly, lesion analysis on patients impaired in the two tasks suggested a common involvement of the Dorso Lateral Frontal cortex (DLF) with no clear lateralization, and Posterior Parietal Cortex (PPC) in both subgroups, but also some specific lesions. In the group impaired in the hand laterality task the lesion extended also to the right S1 and subcortical white matter underlying BA 40, while the one impaired in the motor imagery task showed an involvement of the inferior portion of the left BA 40. Lesion data from patients with BI deficits suggested that the neural correlate for this representation is to be identified in the left temporal lobe, while BSD deficit are most frequently a consequence of a left parietal lesion. More recently, Corradi-Dell'Acqua and colleagues (Corradi-Dell'acqua, Tomasino, and Fink 2009) investigated the neural substrates of the BSD in healthy subjects with fMRI and confirmed the involvement of the left parietal cortex and in particular of the intraparietal sulcus (IPS). Overall, these results support Sirigu and colleagues' model and in particular show that the semantic/lexical and structural knowledge of the body are coded in separate representations that have their own neural correlates.

Now, I will turn discussing two more recently proposed models of body representations that focus specifically on the somatosensory system and, in doing so, postulate the existence of different body schemes according to the different mappings necessary to access full tactile awareness: These models postulate that the coding of tactile stimuli not only occurs with reference to the body surface, but also to the external space. The first model I will present is the one proposed by Medina and Coslett (Medina and Coslett 2010). These authors suggested that the classical BS should be divided in three body representations. The lowest one is a Primary Somatosensory Representation, in other words, the cortical territory activated by the tactile stimulation of a particular body-part. Although the authors do not use the term of Somatosensory Homunculus, the reader can readily recognize it in the authors' description: "provide a depiction of the nature of the stimuli; this representation is altered by use as well as peripheral and central nervous system disruption" (p. 652). The second level is represented by the Body Form representation that is responsible for the localization of tactile stimuli on the body surface. As the previous one, this map is also a distorted representation of the body even though the amount of distortion is not the same as the one in the homunculus. Correct localization of a stimulus on the body requires a rescaling and coupling of the two representations. Before introducing the third level, it is noteworthy that even in healthy subjects, this remapping is not perfect and the brain seems to be unable to compensate for the distortions in the body representations. The Weber illusion is evidence in favor of the fact that only a partial re-scaling is possible. In this famous illusion, blindfolded subjects are presented with two simultaneous tactile stimuli on different body-parts, like the hand (high mechanoreceptors density) and the forearm (lower mechanoreceptors density). Although the distance is kept constant, the perceived distance is longer when they are applied on a body surface with higher density of receptors, which in turns means higher sensitivity. For example, two stimulations will be perceived as more distant when delivered on the hand than on the forearm. This phenomenon suggests that the rescaling between the cortical areas devoted to tactile processing of a particular skin region and the representation of the corresponding body-part is not able to compensate, at least not completely, for the map distortion. Taylor-Clarke and colleagues (Taylor-Clarke, Jacobsen, and Haggard 2004) studied this illusion further and tried to modulate it through distorted visual inputs. Subjects were asked to compare the distance of two couples of tactile stimuli delivered on the finger and on the forearm, before and after a period of exposure to a distorted visual image of their body, where the hand was reduced to half of its size and the forearm enlarged to double its real size. The authors found a significant effect of this visual exposure, as subjects showed a reduction of the Weber illusion (stimuli perceived further apart on the finger than on the forearm) after the visual exposure period. However, it is still to notice that, despite the huge visual distortion, the effect on the tactile task was only of about 1%. Similar effects of visual information on the body form representation come from the phenomenon of “visual enhancement of touch” (Tipper et al 1998; Kenneth et al 2001; Taylor-Clarke et al 2002), which consists of an improved tactile discrimination due to the vision of the stimulated body-part. Here, again, visual distortion of the body can affect the spatial resolution in the tactile modality, and in particular viewing a magnified picture of the touched body-part produces a significant improvement in tactile acuity. Interestingly, Medina and Coslett (2010) offer the Pinocchio illusion (supposed to tackle the BI), and its consequences on the tactile processing shown by de Vignemont and colleagues (de Vignemont, Ehrsson, and Haggard 2005), as evidence of the existence of the Body Form representation and of its tight relation with the Primary Somatosensory Representation.

Finally, the third level of body representation model proposed by Medina & Coslett is the one that permits the localization of touch in the external space, and is called Postural Representation. It integrates visual, vestibular and proprioceptive information into a scheme of the size, shape, as well as the configuration in space of the body. The localization of perceptual stimuli in the external space is not possible if the information about the position in space of the stimulated body-part is not known. The tactile location can so be encoded in an egocentric reference frame. This description clearly makes the Postural Representation the equivalent of the BS in terms of function, although the type of sensory information used to update it is extended from propriocetion alone to other sensory modalities.

It is not clear if the body representations proposed by Medina and Coslett are to be added to a conscious BI and a BSD to form a pentad model. What is clear is that as long as we create a label for each stage of the sensory processing and/or selective deficit, the number of levels of representations within our models will be multiplied, instead of being reduced, and doubts may emerge as to their actual existence (de Vignemont, 2010). One solution could be to consider whether and how many successive stages in the mapping processing can take place as multiple computations performed within a unique body representation. For example, one can imagine that the knowledge about the body shape and size, that is fundamental for the motor control, is represented inside the BS and constantly updated each time a change of these parameters happens. Although this assumption seems logic, it is an assumption and not a scientific fact. There is actually no empirical evidence available nowadays to support the hypothesis that both shape and size are embedded in a single representation (say, the BS). Moreover, additional questions will immediately derive: if we assume that the knowledge of the body metric is inside a body representation, will it be the only body metric, or would each representation have its own metric? Can/should we hypothesize the existence of a metric for action, a metric for perception (and eventually a semantic metric)? We currently lack a satisfactory answer to these questions. The point I would like to underline in this dissertation is that we should orient our efforts towards an operational definition of body representations, which take into account several criteria for circumscribing their properties and functional roles. I will turn discussing this aspect later on (see general discussion).

The last model of body representation I will present has solved the problem of body metric by assuming the existence of a further body representation, the Body Model (BM), which stores this kind of information (Longo, Azañón, and Haggard 2010). In their model, the authors distinguish three classes of processing inside the somatosensory system. A first low-level process is Somatosensation, which is the primary sensory processing of somatic stimuli that occurs in SI and SII. The two higher-level stages are Somatoperception and Somatorepresentation. Somatoperception is defined as "the process of constructing percepts and experiences of somatic objects and events, and of one's own body" (Longo et al, 2010, p.656). Somatoperception allows four fundamental activities of the human being that are the localization of touch on the skin surface, the perception of the metric of object in contact with the body, of the body-parts in the external space and of object in the external space. The ability to localize tactile stimuli on the body surface is explained by the authors as the result of a two stages mapping. First, the tactile stimulus is coded in the neural map of the body (the homunculus), which allows for the detection of the stimulus, but not it's localization. At this stage, the subject knows that he/she has been touched, but only the relative position with respect to other locations inside this map is available. In a second step, the somatotopic location is mapped in a representation of the body surface, that the authors call Superficial Schemata (as originally identified by Head and Holmes, 1911-12). At this stage, a tactile stimulus can be localized on the body. This remapping requires a rescaling since the somatotopic map is highly distorted and a failure of this remapping can bring to a mislocalization of tactile stimuli on the body that respects the arrangement of body-parts inside the somatotopic map. In this respect, supporting results come from Rapp and colleagues (Rapp, Hendel, and Medina 2002) who tested two stroke patients who had a parietal lesion involving, among other structures, SI and SII. Despite the lesion, they were both able to perceive tactile stimulations on the back, as well as on the palm of the contralesional, as well as ipsilesional, hand. However, when asked to point (the eyes open) with the ipsilesional hand toward the tactile stimulation on the contralesional hand, their performance was impaired as compared with both the ipsilesional side (pointing with the contralesional hand toward stimuli on the ipsilesional one) and the control subjects. In particular, they showed a peculiar pattern of results characterized by a proximal shift and compression of the end-points on both the back and the palm of the hand. The authors interpreted this result as a systematic somatosensory reorganization after lesion that preserves the pre-traumatic organization, since relative position of the stimulation is still present, although it is compressed in a new shrunk hand.

A second body representation in Longo and colleagues' model is the Postural Schema that integrates different type of afferent information, such as proprioception and touch, as well as efferent signals about movement, to form a schema of the body posture. This description and name clearly reminds of the BS, a label the authors explicitly avoid employing because of its inconsistent and contradictory usage. The main (and only?) difference between Longo and colleagues' Postural Schema and the Body Schema as I have reviewed it up to now, is that the Postural Schema does not contain any information about the size of the body. Longo and colleagues ground their reasoning on the statement that there is no direct information from the periphery to the cortex that inform the brain about the size of a body-part. While muscles spindles and skin receptors can inform us about the stretching of the skin, or the contraction (i.e., the relative length) of a muscle, no receptors can provide signals about the absolute length of the same muscle for example. At the same time, this information is essential for knowing the position in space of a body-part and as a consequence for an effective interaction with the environment. To solve this problem, the authors suggest the existence of a specific body representation, the Body Model (BM) that stores the metric knowledge about body-parts' size. As a consequence, the localization of body-parts in space is thought to be the result of an interaction between the Postural Schema that specifies the configuration of the different body segments in space, and the BM.

Although I think that knowledge of the metric of the body is essential, and not only for motor control, the existence of the BM is questionable. It is true that mechanoreceptors in joints, muscle tendons or stretch-sensitive receptors in the skin can inform the brain about a change in muscle contraction or skin stretching, but not about the absolute length of the muscle/body-part. This implies that, in order to know the position in space of a body-part, this information have to be integrated with a metric representation; this does not imply, however, that an additional body representation (the BM) exists. Indeed, we can imagine that, to execute actions, the BS itself contains a metric of the body that is the result of a constant update following the body modifications during the entire life. The problem here is not the origin of the body metric (not given directly by receptors but derived in some other ways), which remains problematic for any putative body representation (either BS or BM). From where, indeed, would the BM emerge if there is no peripheral information directly providing the body-part size (see below)? The real problem is whether it logically follows from this observation (size is not directly given by receptors) that body metric is located outside the Postural Schema. As it will be shown in study 1, the BS is a highly plastic representation that is able to adapt to abrupt changes of body size in a short time scale (see study n. 1).

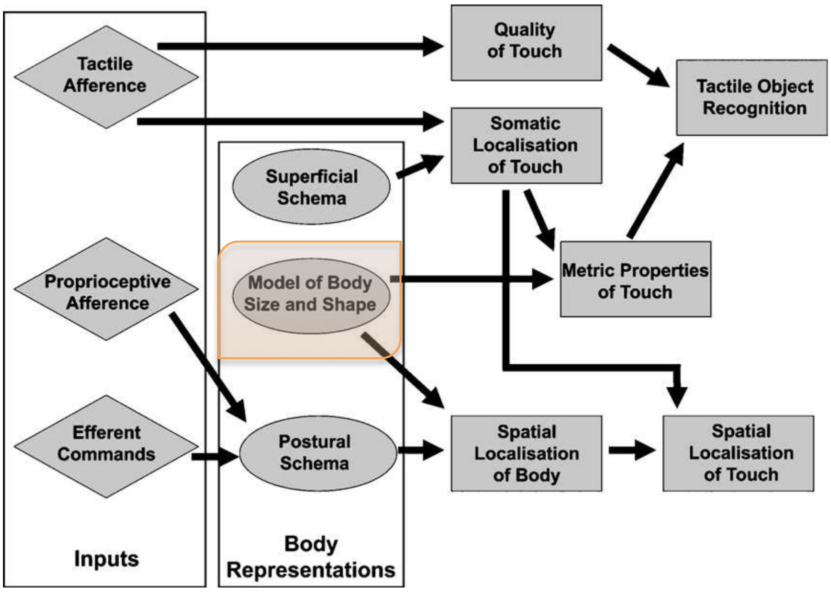

Figure 9. Schematic model of the somatosensation processing. The BM has been highlighted. From Longo et al., 2010

Moreover, the authors themselves must assume that the knowledge of metric properties exists inside the already proposed representations or, at least, that those representations have access to this kind of information. The Superficial Schema, which subserves tactile localization through the remapping from the homunculus, has to have knowledge about the body size. Secondly, the BM seems to be an innate representation, since is not fed by any sensory information (see figure 9). So, where does the BM come from? How such a representation can follow the impressive changes in size the human body goes through?

To strengthen the point that an accurate knowledge of body size is important, the authors bring as evidence the fact that during a period of “great spurt” as adolescence is, young people are often clumsy and that coordination difficulties are related to a peak of growth registered in this phase of life. This only suggests that, if a BM exists, this metric representation is not properly fit to update changes in body size. Again, it is hard to accept that a representation dedicated to body size knowledge is not, in physiological conditions, capable to assure this role. It seems a lot of work for not that much a gain. Moreover, this representation seems to be highly distorted and therefore unable to grant a correct body localization, which is the activity for which the BM is supposed, according to Longo and colleagues, to be essential. The same group indeed showed that when asked to point to memorized landmarks on the hand with a stick, subjects make constant errors compatible with a distorted representation of the arm size and shape. In particular, the fingers are represented as shorter while the hand is represented as larger (Longo et al, 2009). In this study, healthy subjects were asked to make non-ballistic pointing movements to named hand landmarks that have been previously memorized. The type of pointing, as well as the input modality used in this task, would exclude an involvement of the BS. Moreover, the absence of such a distortion when a size-judgment was visually-based (choosing among differently distorted pictures the one the represents the actual hand size) made the authors to conclude that the BI is neither involved, coming to the conclusion that there must be a third representation involved in the task. However, alternative explanations are possible. The authors did not test for a possible role of the memorizing process in the creation of a task-dependent visual imagery of the hand. Second, it is possible that a BI representation is used in both tasks and that the dissociation is the result of a difference between the tasks, not between the representations (see, for task dependent dissociation, Rossetti et al 2001; Kammers et al 2009, 2010). In the picture-choosing task, the richness of the visual information makes the task easier since it can be done also by using a criterion of plausibility of how a hand is shaped and not simply using a representation of our own hand shape. In the memorized pointing task, the absence of online visual information, mainly used in the building of the BI, could be responsible for the observed distortion. Moreover, the fact that subjects were not blindfolded, might have strengthened the importance of visual information and the adoption of visual strategies. To go back to Longo and colleagues' model, another surprising fact is that the BM does not subserve any fundamental process, by itself. It is supposed to contribute to body-parts localization and to the perception of metric properties of tactile objects thanks to the integration with the Postural Schema. It does not seem to be an economic choice. Following this hypothesis, we should have a representation that is innate (while body size changes can be influenced by many external environmental factors), "unfed" (that makes difficult to understand how it can be updated), dramatically distorted (that make difficult to understand how we can perform accurately any of our daily motor actions) and unable to follow normal changes in size like, the growth of our own body. It is, indeed, quite difficult to agree on the need of a BM. Instead, I suggest that a metric of the body is present in the BS and the BI and that the metric properties of the two representations can be differently affected and accessed to, possibly according to the different processing needed to solve a given function, task at hand. Here, I only briefly mention that this notion derives from the dissociation between the dorsal and ventral visual streams (Ungerleider and Mishkin, 1982; Goodale and Milner, 1992) that has been reviewed above (chap 2) and has been extended to the somatosensory domain (Dijkerman & de Haan, 2007). A metric of visual objects is present within each stream, but for different purposes and it seems (more) plausible that a similar principle would also hold for body representations (rather than having an additional, full-purpose body metric representation).

At the end of this review, I want to summarize some of the points that are of interest and that have been approached in my thesis. The context in which my work is embedded is one of the most intensively debated in the neuroscience of the body. As shown in this chapter, different authors have proposed many different body representations, along with names, definitions, and suitable tasks to test them.

Basically, something to be baffled by. However, beyond the confused cloud of labels, some key points are clear and can be addressed experimentally. The first and major point is the plastic feature of the BS. As reported at the beginning of this chapter, the BS is supposed to be a plastic representation (Head and Holmes, 1911-12). Being the representation of body for action, it has to take into account any possible modification in the body state that is relevant for action. Changes in posture are an example. If I want to grasp an object I need to know the position of the hand and arm I want to use to implement the correct trajectory. Arm length can also change: slowly, as in the case of the normal growth, or abruptly, when we use tools. Despite the simplicity of the idea and the fact that it has been proposed more than a century ago, the plasticity of the BS has never been directly tested, and this has been the object of the study n.1. The study n. 3 had the goal to make a step forward in the investigation of the BS plasticity, as we tested the level of specificity of this plasticity and the rules that govern it.

The second point is the relation between BS and BI. I have presented many studies showing double dissociations between the two representations in patients (Paillard et al, 1983; Rossetti et al, 2995, 2001; Anema et al, 2008; Brochier et al, 1994; Halligan et al, 2006). Recent studies also provided evidence in favor of a dissociation in healthy subjects (Kammers et al 2009, 2010) showing that the BI can be modified without affecting the BS. We provided the opposite dissociation by showing that tool-use selectively modify the BS, leaving the BI relatively unaffected (see study n.2). In the same study, we also addressed the issue, raised by Kammers and colleagues (2010), of the importance of the input modality, as well as the output in the methodological approach to the study of body representations. The dissociation between BS and BI is indeed based on the two-routes model of sensory processing assuming that the outcome, that is action or perception, determines the way sensory information is processed or, in our case, which body representation is used. This model led to a methodological approach that used essentially motor versus perceptual tasks. This approach is however simplistic and not immune to dangers. We showed, in study n. 2, that the type of task does not guarantee per se the access to a given body representation.

Operational definition of Body Schema

Body and space representation

The review of more than one hundred years of work about the Body Schema made in the previous chapter shows how difficult it is to reach a consensus on the number, definitions and functions of body representations. However, a fruitful scientific approach should be based on the clearest and most economic possible explanation, which can rise only from clearly defined concepts. With this aim, the first step of my thesis has been to try offering an operational definition of the Body Schema. In particular, I tried to summarize the key features of this representation in such a way that they could be tested in appropriate experimental conditions.

In doing so, the first problem I encountered was the undifferentiated use of the labels Body Schema and Peripersonal Space (PpS) that is often present in the literature.

The origin of this confusion is to be ascribed to the fact that both representations share important features. The PpS is indeed a particular region of space around the body where different sensory information are highly integrated (Rizzolatti, Scandolara, Matelli, and Gentilucci 1981a; Rizzolatti, Scandolara, Matelli, and Gentilucci 1981b;Rizzolatti, Fogassi, and Gallese 1997). It is coded by multisensory neurons that integrate visual, tactile and auditory stimuli into a unique multimodal representation of space that is limited in depth.

In addition, both the BS and the PpS are representation devoted to action and both are shaped by action, as we showed in the two experimental contributions that are presented at the end of this chapter.

Moreover, the Body Schema and the PpS have often been tested using similar paradigms, such as those looking for the effects tool-use may produce over perceptual tasks. Evidence in favor of a plasticity of the PpS comes from both animal and human studies with tool-use. In the following section, I will first address the theoretical issue of the possible independence of these two representations underlying both their common features and differences. In the successive empirical contributions, I tested the hypothesis that the PpS subserves the execution of voluntary actions in space. We used the Cross-modal Congruency Effect (CCE) paradigm (Spence et al 1998) to test the modulation of PpS as a function of an action. The CCE is a measure of the integration between visual and tactile information and in particular of the interference exerted by a visual, task-irrelevant information on the response to a tactile target stimulus. In a classic CCE paradigm, subjects seat holding two objects between thumb and index fingers, one for each hand. Visual stimuli are embedded in the objects, close to each finger. The task is to discriminate as quick as possible the location of a tactile stimulus that can be delivered either on the thumb or the index finger. At about the same time as the tactile stimulus, an irrelevant visual distractor is presented in a congruent or incongruent location. The main effect is that when the visual distractor is presented in an incongruent location, for example close to the index finger while the tactile stimulation is on the thumb, the subjects' performance is worse as compared with the congruent condition. The CCE is the difference in performance (RT or accuracy) between the congruent and incongruent trials. Importantly, the spatial distance between the visual and tactile stimuli modulates the effect, the CCE being stronger at shorter distances. Thus, this paradigm is well suited to measure changes of PPS, which has limited extent in depth around the body. The novelty of our approach consisted in the fact that we used the CCE paradigm in a dynamic situation, where the visual distractors were embedded in a target object subjects were instructed to grasp. As a further innovative aspect, we additionally recorded the kinematics of the grasping movements in order to study the relation between action-related modulations in PPS, as revealed by the CCE, and the action execution itself.

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Peripersonal Space and Body Schema: Two Labels for the Same Concept?

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Abstract To sensibly interact with the environment, like when grasping objects and navigating through space, the brain needs to compute not only target- and environment-related inputs, but also the size and spatial location of the entire body as well as of its parts. The neuronal construction and dynamic updating throughout the entire life of this bodily representation, commonly termed body schema in the literature, appears essential for efficient motor control and skilful tool-use. Meanwhile, recent contributions to the study of spatial multisensory processing have identified the peripersonal space as a particular region surrounding the body that acts as an interface between the body and the environment, for defensive and/or purposeful actions toward objects. In addition, the peripersonal space features plastic properties following tool-use that largely overlap those originally ascribed to the body schema, and have been actually interpreted as reflecting changes in the body schema itself. Here we seek to provide operational definitions and neuronal bases for each of these concepts, questioning whether sufficient evidence exists for them to be considered as the two faces of the same coin.

Keywords Multisensory · Peripersonal space · Body schema · Proprioception · Tool-use

Introduction

The body is a peculiar object of investigation. Different level of conceptualization may lead researchers to study bodily representations from the relatively low-level perspective of sensory and multisensory processing (Brozzoli et al. 2006; Farnè et al. 2003; Maravita et al. 2003; Makin et al. 2008), up to higher-level perspectives about the body as the space for the self (de Vignemont 2007; Jeannerod 2008), as well as different level of body-related consciousness (Bermúdez et al. 1995; Legrand et al. 2007). After Pierre Bonnier's (1905) neuropsychologically grounded intuition about the existence of a sense of bodily space, we owe to Head and Holmes (1911–1912) the notion of body schema. Despite being quite well known, the notion of body schema is not unambiguously referred to in the literature, and it has been previously noticed how this term had been used as a sort of conceptual passe-partout (e.g., Maravita et al. 2003). In particular, the body schema appears difficult to be distinguished (see Holmes and Spence 2004) from the notion of multisensory peripersonal space (Rizzolatti et al. 1981a, b; di Pellegrino et al. 1997) that has been neurophysiologically characterized in detail in the monkey (Duhamel et al. 1997; Fogassi et al. 1996; Graziano and Gross 1995; Rizzolatti and Fadiga 1998) and whose anatomo-functional similarities have consistently been documented in humans (Làdavas and Farnè 2004; Maravita and Iriki 2004; Sereno and Huang 2006; Makin et al. 2007). As the body schema and peripersonal space are both tightly linked to action and because action shapes both spatial and bodily representations, their own destinies have been

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interconnected, recently resulting in a substantial overlap between the two concepts. Here we briefly review the fundamental properties of the peripersonal space in terms of its multisensory nature and its plastic features, mainly related to the use of tools to manipulate distant objects. We then turn to consider the similar basic aspects of the body schema, to assess whether the proposed parallel with peripersonal space should be definitively pushed farther toward a conceptual identity or not.

The Peripersonal Space

The peripersonal space consists of a region immediately surrounding the body, characterized by a high degree of multisensory integration between visual, tactile and auditory information, which differs from farther regions of space. Although we perceive the space as something continuously defined and unitarily represented, as in the Cartesian geometrical definition we are used to, space derives from the "perceptual space" and it is composed by different neuronal representations, each built in relation to the behaviour we can perform in the environment (Farnè et al. 2005a, b). The peripersonal space representation can thus be added to a triadic space taxonomy that can be described following a sensorimotor criterion: the personal space, occupied by the body itself, whose representation is mainly built via proprioceptive and tactile information, but also with the contribution of visual input about body-parts in the space; the extra-personal space, principally based on visual and auditory inputs that convey information from the far space; the reaching space, within the extra-personal space but proximal to the body, functionally defined according to the distance at which an object can be reached by the subject's hand without moving his/her trunk. The peripersonal space, mainly based on the integration of tactile and visual information coming from the body and the space immediately around the body, constitutes a privileged interface for the body to interact with nearby objects.

Neurophysiological Bases of Peripersonal Space in Non-Human and Human Primates

One of the first scientists to formulate the concept of a special area of space around the body was Hediger, director of the Zurich Zoo from 1954 to 1973. In his formulation, this region of space was called "flight zone" and corresponds to a margin of safety around the animal's body (e.g. Dosey and Meisels 1969). When a threatening object enters this safety margin the animal escapes. In a more psychological context, many researchers noted that humans behave as if they had an invisible bubble of protective space surrounding their body. Whenever the proximal space boundary is violated, the person steps away to reinstate the safety margin. The size of this region of space is supposed to increase in a potentially threatening context with respect to friendly company.

With the discovery of bimodal visuo–tactile neurons in monkeys' brain, the peripersonal space found both a more precise definition and its physiological basis (Rizzolatti et al. 1981a). Hyvarinen and Poranen (1974) reported that some neurons in the parietal area 7 of non-anesthetized macaque monkeys were activated by a tactile stimulus delivered onto the tactile receptive field on a specific body-part, as well as by a visual stimulus whenever presented close to the same body-part. However, it is only in 1980s that the systematic studies of Rizzolatti's group (Rizzolatti et al. 1981a, b), revealed the properties and the distribution of these neurons in an anterior region of the monkey brain, namely the ventral premotor cortex (area F4). Most of F4 neurons respond to stimuli in one or two sensory modalities. Accordingly to the particular modality activating the neurons, they were classified as somatosensory, visual or bimodal (visual and somatosensory) neurons. Visual neurons are located rostral to the arcuate sulcus (area 8, or FEF), whereas somatosensory and bimodal neurons are found predominantly caudal to the sulcus (area F4). The parts of the body most represented are the hands and the mouth. According to the location of their visually responding region (i.e., their receptive field, RF), bimodal neurons were subdivided into pericutaneous (54%) and distant peripersonal neurons (46%). The former responded best to stimuli presented a few centimetres from the skin, the latter to stimuli within the animal's reaching distance. The visual RFs were spatially related to the tactile ones. Therefore, an important property of these neurons, as other cells in different multisensory areas (see below) is that the extent of their visual RF is limited in depth to a few centimetres (in most cases from ~ 5 to ~ 50 cm) out of the tactile ones. Moreover, when the arm is moved under the monkey's view, the visual RF follows the body-part, being anchored to the tactile RF of that body-part (Graziano and Gross 1993, 1995). A peripersonal region is similarly coded around the monkey's head. In particular, some neurons in the ventral intraparietal area (VIP) have visuo–tactile receptive fields mostly localized on the animal's face and head. As for other body-parts, VIP neurons may thus build a multisensory representation of the head-centred peripersonal space (Duhamel et al. 1997; Avillac et al. 2005). Through this interconnected network of bimodal areas, as Graziano pointed out, "the visual space near the animal is represented as if it were a gelatinous medium surrounding the body that deforms whenever the head rotates or the limbs move. Such a map would give the location of the visual stimulus with respect to the body surface, in somatotopic coordinates" (see below for the functional role played by peripersonal space).

An important characteristic of the bimodal neurons is the dynamic property of their visual RFs. Iriki's group (Iriki et al. 1996) studied bimodal neurons of the post-central parietal gyrus, somewhat extending into the intra-parietal sulcus, that code for the peripersonal space of the hand-arm in monkeys. They showed their visual RF is not fixed, but can be expanded. Indeed, Iriki and colleagues trained monkeys to use a rake to reach for food pellets placed out of the animal's hand-reaching distance. Following this tool-training, the visual RF of some bimodal neurons coding for the hand peripersonal space were elongated towards the tool-tip, such that the tool appeared to be included within the visual RF. A few minutes after the training, the visually responsive area changed again, apparently shrinking back to its original size. These modifications were not observed if the rake was just passively held by the animal, suggesting that for such a change to occur, the tool has to be actively employed to perform an action. In other words, the dynamic aspect depends on the execution of a specific motor action (Rizzolatti and Fadiga 1998). In a similar vein, Fogassi et al. (1996) also found that the visual RF of F4's visuo–tactile neurons expand when the visual stimulus velocity increases while approaching the cutaneous RF, a property that could be crucial for preparing and/or executing actions towards nearby objects.

Several studies support the existence of a similar representation of the space around the body in humans. In this respect, the study of a neuropsychological condition called 'extinction' (Bender 1952; Brozzoli et al. 2006) provided considerable insight into the behavioural characteristics of multimodal spatial representation in the human brain. Extinction is a pathological sign following brain damage whereby patients may fail to perceive contralesional stimuli only under conditions of double (contra- and ipsi-lesional) simultaneous stimulation, thus revealing the competitive nature of this phenomenon (di Pellegrino and De Renzi 1995; Driver 1998; Duncan 1980; Ward et al. 1994). A number of studies have shown that extinction can emerge when concurrent stimuli are presented in different sensory modalities: a visual stimulus close to the ipsilesional hand can extinguish a touch delivered on the contralesional hand (di Pellegrino et al. 1997). These studies reported the presence of stronger cross-modal visual–tactile extinction when visual stimuli were displayed in the near as compared to the far space, providing a neuropsychological support to the idea that the human brain represents peripersonal space through an integrated multisensory visuo–tactile system. Moreover, as described in monkeys' studies, also in humans the visual peripersonal space remains anchored to the hand when this is moved in another hemi-space, suggesting that peripersonal space is coded in a hand-centred coordinate system (di Pellegrino et al. 1997). As for the hand, a multisensory mechanism is involved in representing peripersonal space in relation to the human head. By showing stronger visual–tactile extinction for homologous (left and right cheek) than non-homologous combinations of stimuli (e.g., left hand and right cheek) we demonstrated the modular organisation of peripersonal space, different regions adjacent to different body-parts being represented separately (Farnè et al. 2005). Further support to this view has recently been provided by neuroimaging findings showing a human parietal face area representing head-centred visual and tactile maps (Sereno and Huang 2006). Finally, we have shown that human peripersonal space also features plastic properties, akin to those shown in the monkey. A similar re-coding of visual stimuli located in far space, as if they were closer to the participants' body, has been documented behaviourally in extinction patients following the use of a rake to retrieve distant objects (Farnè and Làdavas 2000; see also Holmes et al. 2004; Maravita and Iriki 2004; Berti and Frassinetti 2000). In this study, cross-modal visual–tactile extinction was assessed by presenting visual stimuli far from the patients' ipsilesional hand, at the distal edge of a 38 cm-long rake passively held in their hand. The patients' performance was evaluated before tool-use, immediately after a 5-min period of tool-use, and after a further 5–10 min resting period. The authors found that far visual stimuli induced more contralesional extinction immediately after tool-use, than before tool-use. Therefore, near and far space are separately represented and what is near or far is not defined a priori, but functionally depends upon movements that allow the body to interact with objects in space. Several authors have since suggested that tool-use dependent changes in multisensory processing may reflect changes occurring in another brain representation, namely the body schema.

The Body Schema

The body schema is a representation of body-parts' dimensions and positions in the external space whose conception can be traced back to 1883, when Pierre Bonnier suggested the existence of an organized spatial representation (or "spatial sense") of the body. However, the "postural schema" introduced later by Head and Holmes (1911–1912) is universally considered as the first model of a plastic representation of the body. The main proprieties of this representation are to be finalized to action, to be dynamically updated and strictly internally coherent.

Body Schema for Action (Executed and Imagined)

To accurately reach-to-grasp an object the brain needs to compute not only the position, shape and dimension of the target, but also of our own body and, in particular, of the body-part we want to use to execute the action (the arm in our example). The body schema is the representation of the body and its parts the brain uses to this, among other aims. Body-parts' spatial positions and dimensions are computed by combining information coming from different, but essentially somatosensory modalities, such as proprioception, kinesthesia and touch, in a sensory-motor schema. Head and Holmes suggested that the main function of the body schema is to appreciate active and passive movements' execution, in contrast with another representation, a "Superficial Schemata", involved in tactile stimuli localization on the body surface. Despite the complexity of the author's model, essentially this dichotomy will remain in the subsequent literature, bringing to the more commonly used terms of body schema and body image (see below) that, however, do not unambiguously relate to the originally proposed twofaced representation (Paillard 1999; Gallagher 2005). Several studies have been undertaken to provide evidence supporting this idea, and in particular showing the existence of a double dissociation, i.e. the possibility to observe a deficit that is limited to one body representation in a (group of) patient(s), with the inverse pattern being observable in another (group of) patient(s) (Paillard 1999; Cole and Paillard 1995). Deafferented patients, for example, have been shown to be able to localize a touch on their own hand despite a deficit in localizing the hand's position in space, or vice versa. More recent work proposed the existence of at least three different levels in which the body is represented (Sirigu et al. 1991; Buxbaum and Coslett 2001; Schwoebel and Coslett 2005). In these models the body schema is presented in contrast to other body representations such as the body image and the body structural description. The body image is a semantic and lexical representation of the body and its relationship with external objects while the body structural description is a topological map of locations derived primarily from visual information. Contrary to the body schema, these representations operate at a conscious level. Schwoebel and Coslett (2005) have recently tested this model's validity on a large group of stroke patients. The authors developed a battery of tasks to examine the prevalence and anatomic substrates of the body representations' deficits. Patients with a deficit of the body schema succeeded in tests assessing the body image and body structural description, such as to localize isolated body-parts and tactile inputs, to match body-parts by location (a target body-part was visually presented and subjects were asked to point among 3 pictured body-parts the one that was closest on the body surface to the target body-part), to match body-parts by function (e.g., is the knee more akin to the wrist or thumb? What body-part wears the watch?). However, the same patients were impaired in performing tasks impinging on the body schema, such as imagining executing a series of hand movements with different levels of difficulty, and then actually executing those same movements. When response times for both imagined and executed movements were analyzed, the results showed a poor correlation between the two measures, thus suggesting a deficit of the body schema. In the same study, these patients were also unable to perform the hand laterality task that requires a mental rotation of the hand. Patients were presented with a picture of a hand and asked to indicate if the stimulus was a right or a left hand. To solve the task the participant needs to mentally rotate his/her own hand until it matches the position of the stimulus picture, but this was not possible for patients with body schema deficits. The lesion analysis suggested that the body schema is dependent on the dorsolateral frontal cortex and posterior parietal cortex.

Body Schema Representation Is Plastic

As the body changes continuously in position and dimensions throughout life, its cerebral representation needs to be updated for the brain to correctly plan and execute actions. Changes in body-parts' dimension develop relatively slowly, normally taking years, whereas postural changes are quicker and more frequent. Despite this difference in time-scale, both need to be taken into account in the updating of the body schema. Actually, even abnormally fast changes in bodily dimensions are taken into account. Di Russo et al. (2006) showed a rapid cortical reorganization in the primary somatosensory cortex (SI) and in the associative parietal cortex after surgical extension of lower limbs. Acondroplastic dwarf subjects were tested before undergoing a progressive extension (PE) that increased their legs' length by about 15 cm in 6 months. The authors observed an expansion and a shift of the area responding to the foot tactile stimulation in SI 15 days after the PE, which disappeared at the follow-up (6 months later). Crucially, a change in activation was also observed in the superior parietal lobule (SPL) that was still present in the follow-up. SPL is thus suggested to be a crucial area in the parietal cortex involved in coding the relationship between body-parts and between the body and the environment.

The notion that the body schema is plastic can be traced back to the seminal paper by Head and Holmes (1911–1912), where they wrote: "By means of perpetual alterations in position we are always building up a postural model of ourselves which constantly changes. Every new posture or movement is recorded on this plastic schema, and the activity of the cortex brings every fresh group of sensations evoked by altered posture into relation with it. Immediate postural recognition follows as soon as the relation is complete". Two fundamental ideas are exposed here. First, the body schema is essentially a sensorimotor representation, as proprioceptive, kinesthetic and tactile information contributes in building it. Second, its updating takes place at an unconscious level, without needing an attentive effort. So, we don't need to think about the position of our feet at every step, or to our arm length to decide if we can reach for an object. Once the update completed we can consciously report the position of our body, verbally or by pointing to a body-part. In the same paper, Head and Holmes added:

> It is to the existence of these "schemata" that we owe the power of projecting our recognition of posture, movement and locality beyond the limits of our own bodies to the end of some instrument held in the hand. Without them we could not probe with a stick, nor use a spoon unless our eyes were fixed upon the plate. Anything which participates in the conscious movement of our bodies is added to the model of ourselves and becomes part of these schemata: a woman's power of localization may extend to the feather in her hat.

In this plastic feature of the body schema related to tool-use (Maravita and Iriki 2004; Johnson Frey 2003) seems to reside the origin of the potential overlap with the concept of peripersonal space. As reported above, a large amount of studies relating skilful tool-use to the plasticity of the body schema actually refers to findings that pertain to the multisensory processing of peripersonal space. Irikis' findings in the monkey (Iriki et al. 1996), showing enlarged visual RFs of bimodal neurons in the parietal cortex after training with a rake, as well as humans tool-use studies showing changes of multisensory interactions in the peripersonal space of both healthy subjects and neurological patients, have been taken as evidence that tool-use modifies the body schema.

It is unclear, however, to what extent the multisensory effects reported above can be ascribed to a change in the body schema and/or in the peripersonal space processing. We provided more direct evidence for a modification of the body schema following the use of a tool (Cardinali et al. under revision). We recorded in healthy participants the kinematic of free-hand movements before and after training with a mechanical grabber, used to grasp objects. After the use of the tool, subjects performed the same free-hand movement with a different kinematic profile. In particular, they took a longer time to achieve the maximal acceleration, velocity and deceleration and the amplitude of these parameters was reduced. This particular kinematic pattern, involving only the transport component of the movement fits the kinematic difference that is naturally present in subjects on the basis of their morphology. Indeed, when a given movement is performed by subjects that have a different arm length, 'long-arm' subjects will show longer latencies and reduced amplitudes compared to 'short-arm' subjects. When we use a tool the representation of our acting body changes so that the tool becomes a part of the body. This modification takes place rapidly, without requiring learning processes. However, the tool-use dependent plasticity does not vanish immediately, the kinematic changes being present at least up to 15 min after the training with the mechanical grabber. This direct measure of changes in the body schema may thus provide a new sensitive test to verify whether changes in the body schema invariably imply changes in the multisensory processing of peripersonal space, or they can be dissociated.

Internal Coherence of the body Schema

The body schema does not accept any incoherence. This means that when a conflict occurs between two inputs, the brain solves it in the direction of one of them. This mechanism is responsible for many perceptual illusions as, for example, the kinesthetic fusion illusion (Craske and Crawshaw 1974), the rubber hand illusion (Botvinick and Cohen 1998), or the tendon vibration illusion (Lackner 1988). The kinesthetic fusion illusion has been described by Craske and Crawshaw in 1974. Blindfolded subjects were seated with their arms stretched in front of them and separated by a plexiglass panel where a button and a probe were fixed. Subjects had to press the button with their right index finger, which made the probe to touch the left arm. In the experimental condition, the button and the probe positions were not coincident, so that pushing the button delivered a tactile stimulation through the probe that was displaced 12 cm away from the button. This paradigm induces a conflict between the proprioceptive and kinaesthetic information (from the right finger movement) and the tactile stimulus (on the left arm). The brain solves this conflict by making the subject start feeling the two spatial positions as coincident and, consequently, the left arm as being longer than it actually is. Similarly, in the rubber hand illusion (Botvinick and Cohen 1998) a conflict between visual and tactile inputs is solved in favor of the first one, making the subject feeling the seen rubber hand as his/her own hand. The tendon vibration illusion arises when a vibration is applied to the biceps or the triceps of the subject's arm. This vibration elicits a kinaesthetic illusion of passive extension of flexion of the elbow, respectively. If the vibration is applied when the subject is holding with the vibrated hand the tip of his index finger of the opposite hand, an illusion of elongation, or shrinking, of the held finger is induced. de Vignemont et al. (2005) used this illusion and asked subjects to perform a perceptual judgment of the distance of two tactile stimuli delivered on the elongated/shrank finger. They found that the tactile distance feels bigger when the stimulated body-part feels temporarily elongated. Interestingly, the contrary is not true as the perceptual judgment is not affected when the finger is perceived as shorter. The authors explained this result as caused by anisotropy of the body surface: ontogenetic changes are in the direction of a growing body and cannot normally be reversed. The body schema seems to have the ability to quickly change in the direction of a growing body (ontogenetic changes, rapid body-parts elongation, tool-embodiment), but is resistant to modification in the opposite direction as they are not biologically plausible.

Space and Body for Action

May the body schema and the peripersonal space be conceived of as the two faces of the same concept and cerebral representation? The former, classically action related, would be referred to the represented structure and position of the body used by the brain to perform an action; The latter is also action-oriented and refers to the multisensory space immediately surrounding the body, which could be used to perform free hand actions as well as using a functional tool. A large corpus of findings indeed supports the involvement of peripersonal space in the guidance of involuntary defensive movements. In the monkey, electrical stimulation of multisensory areas evokes complex pattern of hand and arm movements compatible with avoidance or defensive reactions, such as withdrawal of the hand, turning of the head or lifting the hand as if to defend the side of the head (Graziano et al. 2002). It would thus be adaptive that responses possibly evoked by multisensory neurons are fast and mainly outside the control of top–down mechanisms. However, these multisensory interfaces might be adaptive also for producing voluntary actions towards objects, such as grasping a glass of water (Gardner et al. 2007; Galletti et al. 2003; Gentilucci et al. 1988; Fattori et al. 2005; Marzocchi et al. 2008). Bimodal neurons properties allow the brain to represent an object in a coordinate system centred on the body that can be continuously up-dated during bodily movements. Remarkably, some bimodal neurons also respond when the arm is voluntarily moved within the reaching space and have been proposed to code goal-directed actions, a question that has been recently addressed in humans in our laboratory (Brozzoli et al. 2009). We provided evidence that voluntarily acting on objects triggers hand-centred remapping of multisensory perception by asking healthy participants to discriminate touches on the hand they used to grasp an object that contained task-irrelevant visual distractors. This provides a measure of how the visual–tactile interaction varies in real time with the action unfolding. Compared to a static condition, the start of the grasping action selectively increased the interference exerted by visual inputs originating from the far target object on tactile stimuli delivered to the grasping hand. This modulation reveals a remapping of the peripersonal space that does not require any tool-use to occur. Therefore, the multisensory peripersonal space may have been selected throughout evolution to drive both involuntary avoidance reactions and voluntary approaching movements. It remains, however, to be established whether the latter form of plastic remapping of space produce changes also at the level of the body schema (e.g., on arm kinematics).

Peripersonal Space and Body Schema: Are They Both Multisensory?

Peripersonal space is multisensory by definition. The construction of this spatial representation relies on the activity of neuronal assemblies that, at the level of single unit in the monkey, display responsiveness to several combinations of auditory, visual, tactile, proprioceptive, thermal and vestibular inputs. Moreover, the principles that govern these cells' activity in response to multiple sensory stimulations seem to conform to those originally described by Stein and Meredith (1993), in the superior colliculus (SC). For example, bimodal stimulation modulates the response of the majority of VIP cells, including bimodal and unimodal ones (Avillac et al. 2007). In both cell types, responses are enhanced or depressed and reflect nonlinear sub-, super-, or additive mechanisms. As for the SC, these responses are maximal when stimuli are in temporal synchrony and spatially congruent. Therefore, at least some of the multisensory integrative rules seem to be shared by the neuronal circuitries devoted to represent the peripersonal and extrapersonal space.

In contrast, the sensory components and integrative mechanisms participating to the construction of the body schema are far less known. The body schema would essentially be fed by tactile, proprioceptive and kinaesthetic information (see Head and Holmes 1911–1912), and would therefore remain a representation of the body possibly extending to something that is in physical continuity with the body (e.g., a tool) (Table 1). In this respect, as suggested by an anonymous reviewer, the body schema might be necessary, but not sufficient, to provide the

Table 1 Summarizing the contribution of different sensory modalities, the functional properties and the neural mechanisms for the peripersonal space and the body schema

	Peripersonal space	Body schema
Sensory inputs	Vision	Proprioception
	Audition	Kinesthesis
	Touch	Touch
Functional properties	Defensive movements Voluntary actions	Body knowledge for action
Neural mechanisms	Parietal–frontal bimodal neurons	Pre-frontal and parietal cortex

skeleton for peripersonal space. While the former would be limited to the body, the latter concerns the space around the body itself, a feature that is not without adding inputs from the visual and/or auditory modality. The multisensory nature of the body schema, at least in these terms, appears thus questionable, thus possibly providing a theoretical framework for their distinction (Table 1).

Distinguishing Peripersonal Space from Body Schema

Overall, the plastic features of spatial and bodily representations, together with their involvement in motor control, have raised the possibility that the peripersonal space and the body schema are tightly related concepts, if not a unique one. The central point is to understand how the two concepts of peripersonal space and body schema are operationally separable. Considering the several parallels drawn above among the findings reported here, those related to the plastic effects of tool-use strongly speak in favour of unifying the body schema and the peripersonal space. Although clear evidence is not yet available to definitively support either their dissociation or their association, it is logically conceivable that a modification of one of them may occur leaving the other unchanged. In this respect, two issues are worth considering here to provide theoretically and experimentally testable approaches for their dissociation: physical continuity and time.

On the basis of the different sensory contributions to either representation (as reported above), the physical continuity with the body would be crucial to induce changes in the body schema, but not the peripersonal space. Suppose one tests the visual–tactile effects of acting in the far space by using a remotely controlled device (like in telemedicine) that produces physical consequences on the environment without any visual continuity between the controlled device and the spatial location acted upon. Provided that some sort of casual relationships are preserved between the actions required to operate the device and their distal consequences, the peripersonal space would likely to be affected by this manipulation, while the body schema should be relative unaffected. The question would be how the body schema would be appropriately tested. We suggest that kinematics of bodily movements provides a sensitive measure of the body schema and its plastic changes. In the latter example, one could hypothesise that multisensory effects could be detected far from the operated device (revealing changes in peripersonal space processing) whereas no kinematic change should be present in the way the device is operated, or when performing free-hand actions after the use of the device.

Another possible framework within which a differentiation between the two action-related representations could be demonstrated is by taking time into account. In particular, the time-course of their modifications is both in terms of latencies and duration. If the two representations are separable concepts and based on different neural mechanisms, we could expect a different latency for changes of the body schema to take place with respect to those occurring in the peripersonal space. Similarly, the duration of the respective modifications could differ. In particular, one can imagine a tool-use protocol where both kinematic and perceptual effects are assessed at regular intervals during the training (see also Holmes et al. 2007). Both kinematic modifications and visuo–tactile interactions could also be assessed after the tool-use training to investigate whether they are dissociable on the basis of their lasting duration. In this respect, the temporal dimension could provide an alternative basis to independently test the dissociation–association issue between these spatial representations.

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Grasping actions remap peripersonal space

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The portion of space that closely surrounds our body parts is termed peripersonal space, and it has been shown to be represented in the brain through multisensory processing systems. Here, we tested whether voluntary actions, such as grasping an object, may remap such multisensory spatial representation. Participants discriminated touches on the hand they used to grasp an object containing task-irrelevant visual distractors. Compared with a static condition, reach-to-grasp movements increased the interference exerted by visual distractors over tactile targets. This remapping of multisensory space was triggered by action onset and further enhanced in real time during the early action execution phase. Additional experiments showed that this phenomenon is hand-centred. These results provide the first evidence of a functional link between voluntary object-oriented actions and multisensory coding of the space around us. *NeuroReport* 20:913–917 © 2009 Wolters Kluwer Health | Lippincott Williams & Wilkins.

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Introduction

The representation of the space near the body, termed 'peripersonal' space (PpS) [1,2], relies on multisensory processing, both in human and non-human primates. In monkeys, bimodal neurons in parieto-frontal and subcortical structures code for tactile events on a body part (e.g. the hand) and visual events near that body part, thus giving rise to body-centred representations of PpS [3–6]. In humans, a functionally homologous coding of PpS is largely supported by behavioural studies showing stronger visuotactile interaction in near rather than far space in brain-damaged [7–9] and healthy individuals [10–13]. For example, visual events occurring in the immediate proximity to the body induce more severe tactile extinction than farther ones [7–9]. Recent functional neuroimaging studies further support the existence of similar multisensory integrative structures in the human brain [11–13].

Despite the large body of knowledge accumulated across species on the multisensory properties of PpS, little is known about its function, and this issue has never been directly assessed in humans. By acting as an anticipatory sensorimotor interface, PpS may serve early detection of potential threats approaching the body to drive involuntary defensive movements [3]. The same anticipatory feature, however, may also have evolved to serve voluntary object-oriented actions [1,2,14]. Here, we tested the latter hypothesis by assessing the effects of grasping objects on the multisensory coding of PpS.

In Experiment 1, we modified a cross-modal paradigm [10], whereby participants indicate the elevation (up or down) of a tactile target delivered to a finger (index or thumb), while a visual distractor is presented at either congruent or incongruent elevation (Fig. 1). We then conducted three experiments in which participants were additionally required to grasp the object in which the visual distractors were embedded. Although the perceptual task was always performed on the right hand, the motor task was performed by either the right (Experiments 2 and 4) or left (Experiment 3) hand. This simple manipulation is crucial in two respects: it equalizes attentional demands for the target object in the stimulated and the nonstimulated hand actions, and it allows assessing whether any modulation of multisensory processing is hand-centred.

Experimental procedures

Participants

Fifteen healthy participants (nine men, mean age 27 ± 5 years) took part in Experiments 1, 19 (10 men, mean age 26 ± 6 years) in Experiments 2 and 3, and 16 (8 male, mean age 25 ± 3) in Experiment 4. All gave their verbal informed consent to take part in this study, approved by the local INSERM Ethics Board.

Supplementary data are available at The NeuroReport Online (*http://links.lww.com/A1251*; *http://links.lww.com/A1250*; *http://links.lww.com/A1249*; *http://links.lww.com/A1248*; *http://links.lww.com/A1247*; *http://links.lww.com/A1246*)

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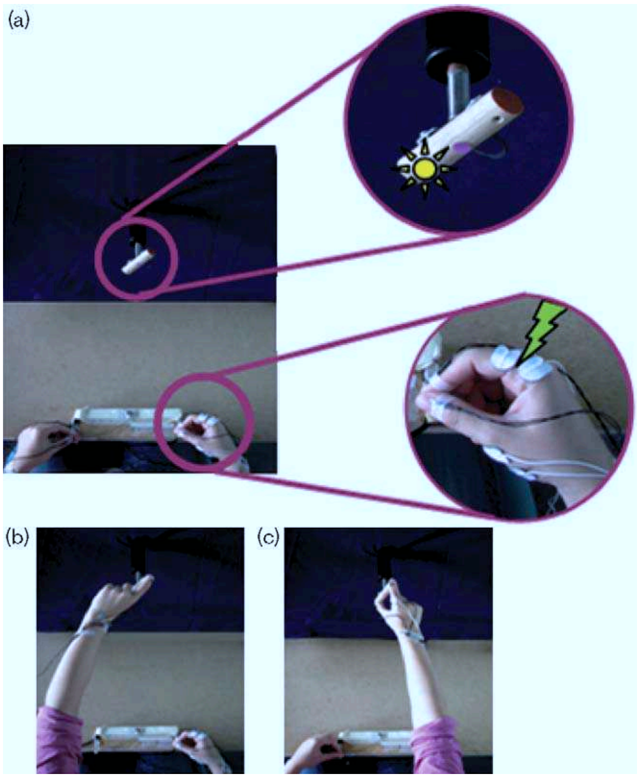
Fig. 1



Experimental setup. (a) Bird's eye view of the participant facing the cylinder (upper inset) with both hands in a pinch-grip position (lower inset). Electro-cutaneous targets (green zap) were delivered to the index finger (up) or thumb (down), while a visual distractor (yellow flash) could be presented from either the same (congruent, not shown) or different (incongruent) elevation. Grasping the clockwise tilted object required an inward wrist rotation of the left hand (b) but an outward wrist rotation of the right hand (c), the opposite pattern being required for the anticlockwise orientations.

Apparatus

A cylinder (7-cm height, 1.7-cm diameter) was presented in one of four orientations (18 and 36° clockwise or anticlockwise) 47 cm from the participant's hand. Visual distractors consisted of an LED flash (200 ms) delivered concurrently with the electro-cutaneous stimulation (see below), from either the top or the bottom extremities of the cylinder (Fig. 1). Neurology electrodes were used to present suprathreshold (100% detection accuracy) electro-cutaneous stimuli consisting of squared-wave pulse (100 μs, 400 V) delivered by constant-current stimulators (DS7A, Digitimer Ltd., Welwyn Garden City, Hertfordshire, UK) either on the index finger (up) or thumb (down) of the right hand. Participants discriminated tactile targets by releasing one of two foot pedals. The participants' eye movements (EyeLink-II, SR Research, Mississauga, Ontario, Canada; SMI) and spatial position of their grasping hand (Optotrak 3020, Northern Digital Inc., Waterloo, Ontario, Canada) were recorded online.

Design and procedure

In Experiment 1, participants performed only the perceptual task consisting of a speeded discrimination (up or down) of tactile stimulation regardless of the task-irrelevant distractor (the upper or lower LED in the cylinder). In Experiments 2, 3 and 4, participants additionally performed a motor task that consisted grasping the cylinder along its longitudinal axis with the index and thumb (precision grip, for details see movies 1–6 in supplementary data). An auditory signal warned the participant about the start of the trial, followed after a variable delay (1500–2200 ms) by a second auditory signal constituting the 'go' for the motor task. The motor task was performed using the stimulated (right) hand in Experiments 2 and 4, and the nonstimulated (left) hand in Experiment 3. The visuotactile stimulation could be delivered: (i) before movement start (Static condition) or (ii) at movement onset (action Start condition) or (iii) during the early phase of movement execution (action Execution condition). These temporal conditions were run across blocks in Experiments 2 and 3, and were fully randomized in Experiment 4. At the beginning of each trial, the tip of the thumb and index finger of each hand were kept in a closed pinch-grip posture on a start switch, whose release triggered the visuotactile stimulation in the Start and Execution conditions (0 and 200 ms delay, respectively).

Results

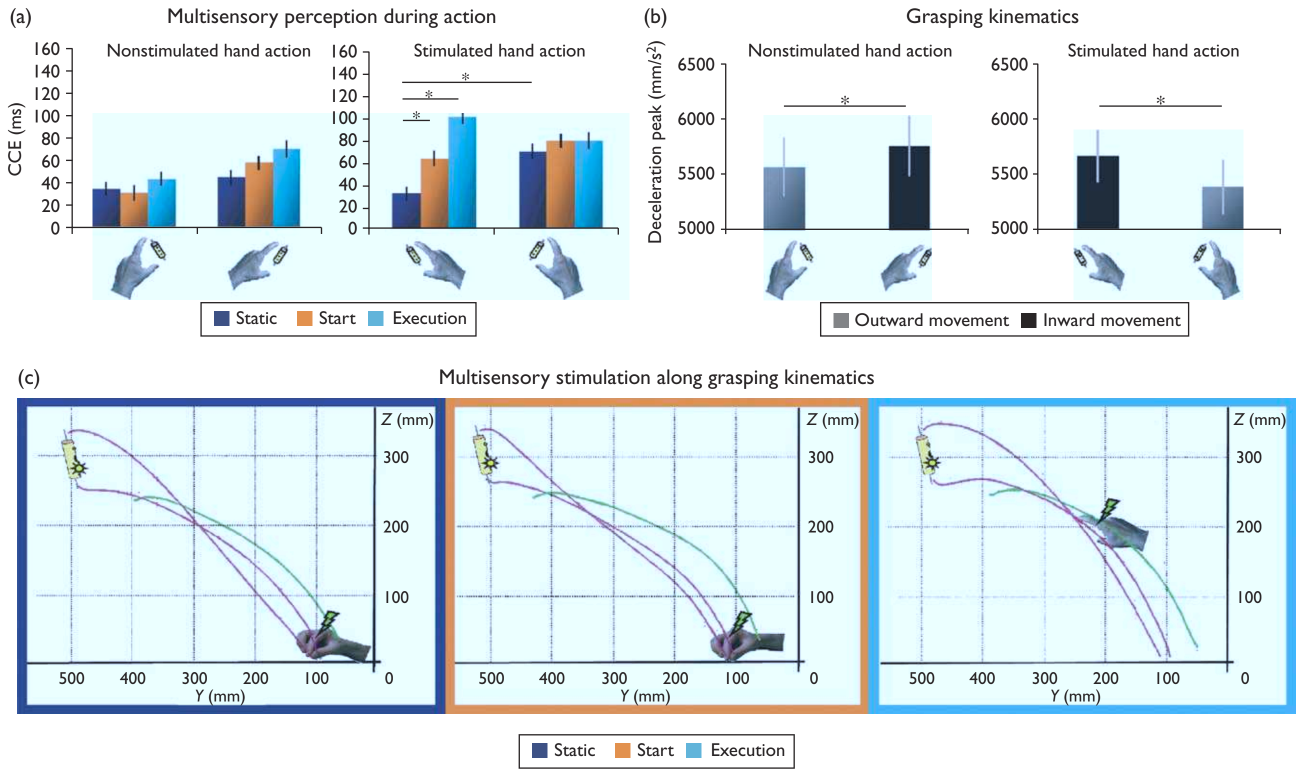
Multisensory interplay without action

When action was not required (Experiment 1), participants proved faster in responding to congruent (360 ms) than incongruent [394 ms; $t(14) = 4.99$, $P < 0.001$] trials, thus extending the typical cross-modal congruency effect (CCE) finding to a situation in which visual distractors were far from the stimulated hand [10]. Hereafter, the dependent variable will be the CCE, calculated as the (reaction times, RTs) difference between incongruent and congruent trials, in that it quantifies the strength of the interaction between visual and tactile inputs (similar trends were found on accuracy). In the absence of action, the CCE varied as a function of object orientation with stronger visuotactile interaction for clockwise (43 ms) rather than anticlockwise tilted object [24 ms; $t(14) = 2.15$, $P = 0.049$].

Action-dependent multisensory interplay

In the Static condition of Experiment 2, before the stimulated hand started to move, the CCE was again stronger when the object was tilted clockwise (66 ms) than anticlockwise [51 ms; $F(1,18) = 6.43$, $P = 0.021$]. Crucially, a modulation of the CCE was observed as soon as the stimulated hand started the action: Fig. 2a shows that the CCE changed on-line with action specifically for the objects oriented anticlockwise [$F(2,36) = 4.37$, $P = 0.020$]. For these orientations, the CCE was stronger when visuotactile stimuli were delivered at action Start

Fig. 2



Real-time modulation of visuotactile processing. (a) Bar plots (with SEM) show the modulation of cross-modal congruency effect (CCE) as a function of grasping hand and object orientation. (b) Movement deceleration peak, similarly modulated by object orientation across hands. (c) Mean movement trajectory of the wrist (green line) and the thumb and index fingers (purple lines). Hand position is schematically illustrated along the trajectory at the time when the tactile stimulus (green zap) was presented. *Refers to significant differences between conditions.

(63 ms) than in the Static condition (31 ms; $P = 0.037$). The CCE further increased during the Execution phase of the action (100 ms; $P < 0.001$ with respect to the Static condition; $P = 0.09$ with respect to the Start condition). Importantly, when the very same grasping action was performed by the nonstimulated hand (Experiment 3), no modulation of the CCE was observed (Fig. 2a), either in the Start or Execution condition compared with the Static condition.

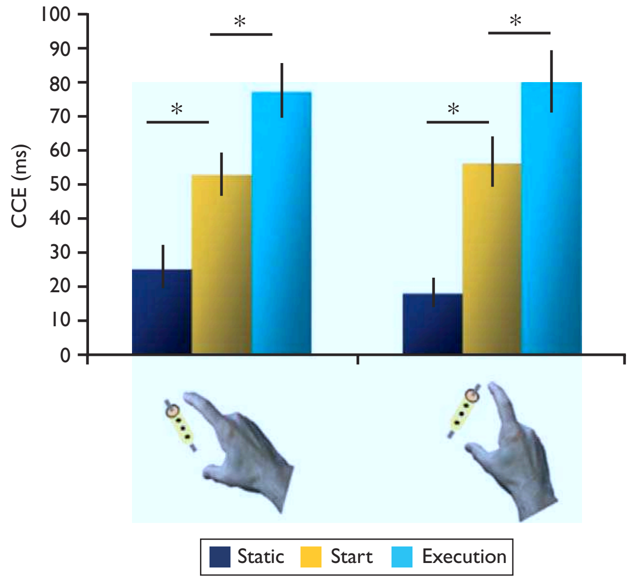
Experiment 4 further corroborated the finding that the action modulates the visuotactile interaction [$F(2,30) = 16.51$, $P < 0.001$]. Furthermore, in this fully interleaved design, the CCE was stronger at the action Start (55 ms) than in the Static condition (22 ms; $P = 0.026$), and in addition, this modulation emerged irrespective of object orientation. As shown in Fig. 3, the action-dependent modulation of the CCE was further increased during the Execution phase (79 ms), with respect to both the Start ($P = 0.022$) and the Static conditions ($P < 0.001$).

Grasping kinematics

To further establish multisensory motor relationships, we analysed the kinematic pattern of all reach-to-grasp movements. Comparison between Experiments 2 and 3 served the important purpose of controlling that hand-related difference between the on-line modulations of action over the CCE were not because of differences between hands kinematic patterns. In addition, through kinematic analyses, we tested for possible parallels between the motor and perceptual performance [15]. Depending on which hand performed the grasping (left or right), the object orientation imposed specific patterns of wrist orientation: clockwise and anticlockwise object orientations required, respectively, outward and inward movements of the right hand (for details see movies 1–2 in supplementary data). The reverse was applied to the left hand (for details see movies 4–5 in supplementary data).

Results of Experiments 2 and 3 showed an effect of object orientation on grasping kinematics. Crucially, however, the overall kinematic pattern proved remarkably similar for the two hands, both for the reaching and grasping components. Object orientations modulated motor RTs to the 'go' signal: it took more time for participants to start the action when the object had to be grasped with an inward (425 ms) than an outward wrist rotation [418 ms; $F(1,17) = 6.80$, $P = 0.018$]. In addition, as shown in Fig. 2b, deceleration peaks for both hands

Fig. 3



Grasping actions remap peripersonal space. Results from Experiment 4. Bar plots (with SEM) report the cross-modal congruency effect (CCE) increase at action Start (55 ms) and Execution (79 ms) compared with the Static condition (22 ms). * Refers to significant differences between conditions.

were more pronounced for inward ($-5709\,\mathrm{mm/s^2}$) than outward movements [$-5474\,\mathrm{mm/s^2}$; $F(1,17) = 23.19$, $P = 0.0002$]. Irrespective of which hand performed the task, acceleration peaks were higher when participants grasped the object with an inward ($6337\,\mathrm{mm/s^2}$) rather than an outward [$6233\,\mathrm{mm/s^2}$; $F(1,17) = 6.46$, $P = 0.021$] movement. The same tendency was present for the velocity peak [1267 mm/s and 1274 mm/s for inward and outward movements, respectively; $F(1,17) = 3.75$, $P = 0.069$]. Peak latencies were not modulated by object orientation with the exception of the acceleration peak, which was anticipated for inward (156 ms) than outward movements [160 ms; $F(1,17) = 5.81$, $P = 0.028$]. Kinematics of the grasping component of the movement showed little influence of the perceptual task.

In Experiment 4, kinematics of the reaching movement was less affected by object orientation. First, motor RTs did not differ between inward and outward movements (377 and 371 ms, respectively). Second, the remaining kinematic parameters were not modulated by object orientation [except the acceleration peak, differing between inward ($8928\,\mathrm{mm/s^2}$) and outward movement, $8690\,\mathrm{mm/s^2}$; $F(1,14) = 5.15$, $P = 0.04$].

Discussion

These findings provide the first evidence that purposefully acting on objects links initially separated visual and somatosensory information, updating their interaction as a function of the required sensory motor transformations. When performing an action, our brain updates the relationship between visual and tactile information well before the hand touches the object. This perceptual reweighting is already effective at the very early stage of the action and seems to be continuously updated as action unfolds. This is clearly illustrated by the fact that from the very start of the action, the task-irrelevant visual information located on the to-be-grasped object interacts more strongly with the tactile information delivered on the hand that will eventually grasp the object. The specificity of such visuotactile reweighting for a given hand while naturally grasping an object confirms the hand-centred nature of the PpS [16–19], and reveals that tool use is not necessary for the human brain to remap space [19]. In addition, it critically extends this property to ecological and adaptive dynamic situations of voluntary manipulative actions, thus pointing to a fundamental aspect of multisensory motor control. By showing comparable pattern of movements across the grasping hands, the kinematics results rule out the possibility that the effector-specific increase of the CCE could merely reflect a difference between the motor performances of the two hands.

The modulation of the visuotactile interaction induced by action, limited to the objects oriented anticlockwise in Experiment 2, was clearly present for all object orientations in Experiment 4, thus fully supporting our hypothesis that voluntary grasping actions affect multisensory perception on-line. In addition, kinematic results were remarkably associated with the perceptual modifications in both the experiments. In Experiment 2, in which the perceptual reweighting was selective for inward object orientation, the kinematic differed between inward and outward reaching movements, in a direction that seemed reflecting more important wrist rotation required for hand pronation [20]. In Experiment 4, the perceptual reweighting was present for all object orientations and the associated kinematics was comparable across inward and outward rotations, thus paralleling, again, the perceptual modulation of action-dependent multisensory remapping. This parallel between movement kinematics and the CCE performance strengthens the functional link between multisensory coding of the hand-centred space and voluntary actions.

Peripersonal multisensory space may serve involuntary defensive reactions in response to objects approaching the body [3,6]. However, here we considerably add to this view by showing that such multisensory motor interface may be functionally involved in voluntary control of actions that bring the body towards objects. This fits well with the functional properties of visuotactile neurons documented in parieto-frontal circuits that present spatially aligned visual and tactile receptive fields for a given body part [1–6,21]. This feature allows bimodal neural systems to represent an object in a body-centred reference frame and to be continuously updated during bodily movements. This multisensory spatial representation has been suggested to serve involuntary defensive movements, because electrical microstimulation of some bimodal areas in the monkey brain [3] elicits stereotyped arm or face movements that are compatible with defensive behaviour. Remarkably, however, some bimodal neurons also respond when the arm is voluntarily moved within reaching space [14,15,*22*,23], and have been previously proposed to code goal-directed actions [1,*2*,*22*]. Neurophysiological studies on monkeys have shown activation in the posterior parietal cortex during grasping, in the early phase of the action when the hand has not yet reached the object. The activation gradually shifts towards the somatosensory cortex when the hand enters in contact with the object [14]. Finally, the on-line enlargement of the visual receptive fields of bimodal neurons in response to approaching objects [6] or tool use [17–19,*24*,25] also emphasizes the dynamic nature of their multisensory space coding, providing converging evidence for the involvement of the bimodal system in dynamic updating of the PpS. The multisensory motor neural machinery acting as an anticipatory interface between the body and nearby events may thus have been selected throughout evolution to drive both involuntary avoidance reactions and voluntary approaching movements, with common adaptive advantages for defensive and manipulative actions.

Conclusion

Voluntarily acting on objects triggers a hand-centred remapping of multisensory spatial processing that parallels action requirements and is regulated in real time as action unfolds.

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Action-specific remapping of peripersonal space

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ABSTRACT

Peripersonal space processing in monkeys' brain relies on visuo-tactile neurons activated by objects near, not touching, the animal's skin. Multisensory interplay in peripersonal space is now well documented also in humans, in brain damaged patients presenting cross-modal extinction as well as in healthy subjects and typically takes the form of stronger visuo-tactile interactions in peripersonal than far space. We recently showed in healthy humans the existence of a functional link between voluntary object-oriented actions (Grasping) and the multisensory coding of the space around us (as indexed by visual–tactile interaction). Here, we investigated whether performing different actions towards the same object implies differential modulations of peripersonal space. Healthy subjects were asked to either grasp or point towards a target object. In addition, they discriminated whether tactile stimuli were delivered on their right index finger (up), or thumb (down), while ignoring visual distractors. Visuo-tactile interaction was probed in baseline Static conditions (before the movement) and in dynamic conditions (action onset and execution). Results showed that, compared to the Static baseline both actions similarly strengthened visuo-tactile interaction at the action onset, when Grasping and Pointing were kinematically indistinguishable. Crucially, Grasping induced further enhancement than Pointing in the execution phase, i.e., when the two actions kinematically diverged. These findings reveal that performing actions induce a continuous remapping of the multisensory peripersonal space as a function of on-line sensory–motor requirements, thus supporting the hypothesis of a role for peripersonal space in the motor control of voluntary actions.

1. Introduction

The representation of the space near the body, termed 'peripersonal' space (Rizzolatti, Fadiga, Fogassi, & Gallese, 1997; Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981), relies on multisensory processing both in human and non-human primates. In monkeys, bimodal neurons have been described in inferior parietal areas (Hyvärinen & Poranen, 1974) and premotor cortex (Duhamel, Colby, & Goldberg, 1998; Fogassi et al., 1996; Graziano & Cooke, 2006; Graziano & Gross, 1995). These neurons have the characteristics to be activated by visual as well as somatosensory stimulations with a higher activity for closer than farther visual stimuli. The activity of these cell assemblies across parieto-frontal and subcortical structures codes for tactile events on a body-part (e.g., the hand) and visual events near that body-part, thus giving rise to body-centred representations of peripersonal space (Gentilucci, Scandolara, Pigarev, & Rizzolatti, 1983; Rizzolatti et al., 1981, 1997; see for review Rizzolatti, Fogassi, & Gallese, 2002). In humans, a functionally homologous coding of peripersonal space is largely supported by behavioural studies, showing stronger visual–tactile interaction in near than far space in brain-damaged (Brozzoli, Demattè, Pavani, Frassinetti, & Farnè, 2006; di Pellegrino, Làdavas, & Farné, 1997; Farnè, Demattè & Làdavas, 2005; Farnè, Pavani, Meneghello, & Làdavas, 2000; Làdavas & Farnè, 2004) and healthy individuals (Bremmer, Schlack, Duhamel, Graf, & Fink, 2001; Pavani & Castiello, 2004; Spence, Pavani, & Driver, 2004; Spence, Pavani, Maravita, & Holmes, 2004). The investigation in neurological patients, for example, revealed that visual events occurring in the immediate proximity to the body induce more severe visual–tactile extinction than farther events (Brozzoli et al., 2006; Farnè et al., 2000). Similarly, in healthy individuals, visual–tactile interaction has been shown to be stronger when visual information is presented close to the body than far from it (Spence, Pavani, & Driver, 2004; Spence, Pavani, Maravita, et al., 2004). In addition to behavioural evidence, recent functional neuroimaging and electrophysiological studies support the existence of similar multisensory integrative structures in the human brain (Bremmer, Schlack, Duhamel, et al., 2001;

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Bremmer, Schlack, Shah, Zafiris, & Kubischik, 2001; Makin, Holmes, & Zohary, 2007; Sarri, Blankenburg, & Driver, 2006; Sereno & Huang, 2006).

Despite the large body of knowledge accumulated across species on the multisensory properties of peripersonal space, little is known about its function as this issue has been assessed in humans only recently (Brozzoli, Pavani, Urquizar, Cardinali, & Farnè, 2009; Cardinali, Brozzoli, & Farnè, 2009). Two not mutually exclusive hypotheses have been proposed on the basis of the neurophysiological findings in the monkey. By acting as an anticipatory sensorimotor interface, peripersonal space may serve early detection of potential threats approaching the body to drive involuntary defensive movements (Graziano & Cooke, 2006). The most direct evidence in favour of this hypothesis is the result of cortical stimulation studies. When multisensory areas where visuo-tactile neurons have been found (Graziano & Cooke, 2006) are electrically stimulated, a pattern of movements is elicited that is compatible with defensive arm movements and withdrawing of the arm or the head. Analogously, in humans, corticospinal excitability during motor preparation has been shown to be modulated by visually approaching objects in a hand-centred fashion (Makin et al., 2009).

The same anticipatory feature, however, may have also evolved to serve voluntary object-oriented actions (Galletti, Kutz, Gamberini, Breveglieri, & Fattori, 2003; Gardner, Babu, Reitzen, Ghosh, & Brown, 2007; Rizzolatti et al., 1981, 1997). In support to this view are the results of single units recording studies showing the motor properties of both parietal (Gardner et al., 2007; Hyvärinen & Poranen, 1974; Leinonen, 1980; Mountcastle, Lynch, Georgopoulos, Sakata, & Acuna, 1975) and periarcuate (Gentilucci et al., 1983; Rizzolatti & Gentilucci, 1988; Rizzolatti et al., 1981, 1987) visuo-tactile neurons. In particular, the visual sensory activation of bimodal neurons seems to be enhanced whenever a reaching movement is performed towards an object (Godschalk, Lemon, Kuypers, & van der Steen, 1985). Such a parieto–frontal network would thus compute the sensory–motor transformations that allow a body-centred coding of space. This, in turn, could be useful for the execution of voluntary actions toward objects (e.g., Fogassi et al., 1992). Recently, we provided evidence in humans of an involvement of the peripersonal space representation in the execution of a Grasping (Brozzoli et al., 2009). When compared to a Static (no action) condition, the initiation of a Grasping movement increased the interaction between visual inputs originating from the to-be-grasped object and tactile inputs delivered to the Grasping hand. This action-dependent multisensory remapping was further enhanced during movement execution when the hand was brought towards the object, but still well before any hand-object contact. Notably, when the stimulated right hand remained still while the left (unstimulated) hand performed the same action these modulations of the multisensory interactions no longer emerged, suggesting that the observed effect was strictly hand-centred. These hand-centred effects of action on multisensory perception support the role of peripersonal space in voluntary object-oriented actions in humans.

In the present study, we took a step forward in the understanding of the functional link between peripersonal space coding and voluntary control of action by testing whether different object-oriented actions would induce different on-line modulations of multisensory coding of peripersonal space. We hypothesized that, if peripersonal space serves the control of voluntary object-oriented actions, action-dependent multisensory remapping should be more important whenever the action to be performed requires relatively more complex sensory–motor transformations. Two hand actions that differ clearly in this respect are reach-to-point and reach-to-grasp. When Pointing the hand (closed in a fist configuration) towards an object without touching it, the brain needs to take into account only object's spatial position relative to the acting body-part (a so-called extrinsic object property; Jeannerod, 1986, 1988). In contrast, when Grasping the same object with the hand, the brain needs to take into account the spatial position of the target object with respect to the Grasping hand (extrinsic object properties), as well as the shape, size of the target object (intrinsic object properties; Jeannerod, 1986, 1988). In addition, because Grasping requires hand-object contact by definition, the intrinsic object properties determine the available landing surface for the fingers and the appropriate wrist orientation for achieving an optimal functional grip on the object. The pre-shaping of the hand (grip component) is smoothly implemented in the reaching phase (transport component), while the hand approaches the object (see Castiello, 2005, for a review). Therefore, while both Pointing and Grasping are composed by a reaching phase during which the hand is brought in the object's vicinity, the two actions are substantially different in the final part of the movement, with additional sensorimotor transformations implemented selectively for Grasping movements.

To test our prediction that action-dependent multisensory remapping is modulated as a function of the sensorimotor transformations complexity, we contrasted the visual–tactile effects produced by performing a relatively simple action (Pointing) with those produced by performing a more complex action (Grasping). In the former condition, participants were asked to reach a target object with their right hand without touching it, keeping a fist hand-configuration (with a closed index–thumb pinch-grip) along the entire movement. In the latter condition, participants reached and grasped the object using a precision grip with the same right hand. Kinematic recording was used to compare the reaching phase of both actions. Visual–tactile interaction was measured on-line in both conditions, by asking participants to discriminate the elevation of tactile stimuli delivered on either the index finger (up) or thumb (down) of the acting hand while ignoring visual distractors embedded into the target object.

2. Materials and methods

2.1. Participants

Sixteen neurologically healthy participants (8 male, mean age 25 year old, ±4) took part in the experiment. Participants had normal or corrected-to-normal visual acuity and reported normal tactile sensitivity. All participants gave their verbal informed consent to take part in this study, which was approved by the local INSERM U864 ethics board.

2.2. Apparatus

The target object was a wooden cylinder (7 cm height, 1.7 cm diameter) located at a distance of 47 cm from the starting position of the participant's hands, at eye-level (Fig. 1a). Two red LEDs were used to present visual distractor stimuli. These were embedded into the cylinder, each at 1 cm from the cylinder's extremities. Visual distractors consisted of a single flash (200 ms) from either the top or bottom LED embedded into the cylinder, delivered concurrently with the electro-cutaneous stimulation (see below). A dot (1 cm diameter) was marked in the center of the cylinder (between the two LEDs) to serve as visual fixation (Fig. 1a, upper circle). To ensure that subjects planned a new action on each trial, the cylinder was unpredictably rotated manually from behind the wooden panel into one of four different orientations: 18° or 36° from the vertical position, in clockwise or anti-clockwise directions, around the virtual axis perpendicular to the longitudinal axis of the cylinder and passing through the fixation point. Disposable neurology electrodes (700 15-K, Neuroline, Ambu) were used to present supra-threshold electro-cutaneous stimuli. Tactile target stimulation consisted of squared-wave single pulse (100 μs, 400 V) delivered through constant-current electrical stimulators (DS7A Digitimer Ltd., UK) either on the index finger (upper stimulation) or on the thumb (lower stimulation) of the right hand (Fig. 1a, lower circle). With respect to the classical static studies adopting the cross-modal congruency task, here electrodes were fixated on the acting hand and stayed attached to it during the duration of the action movement. Electro-cutaneous target intensities were set out individually for each subject and stimulated location, so that participants could detect 100% of the stimuli in a serie of ten trials for index finger and thumb [thumb mean current (s.e.m.) = 11.0 mA (0.6); index finger mean current 11.0 mA (0.5)]. Participants were instructed to respond to the tactile target as fast as possible by releasing one of two foot-pedals (Herga Electric Ltd., England). The real-time spatial position of the participant's Grasping hand was recorded by means of an Optotrak 3020 sys-

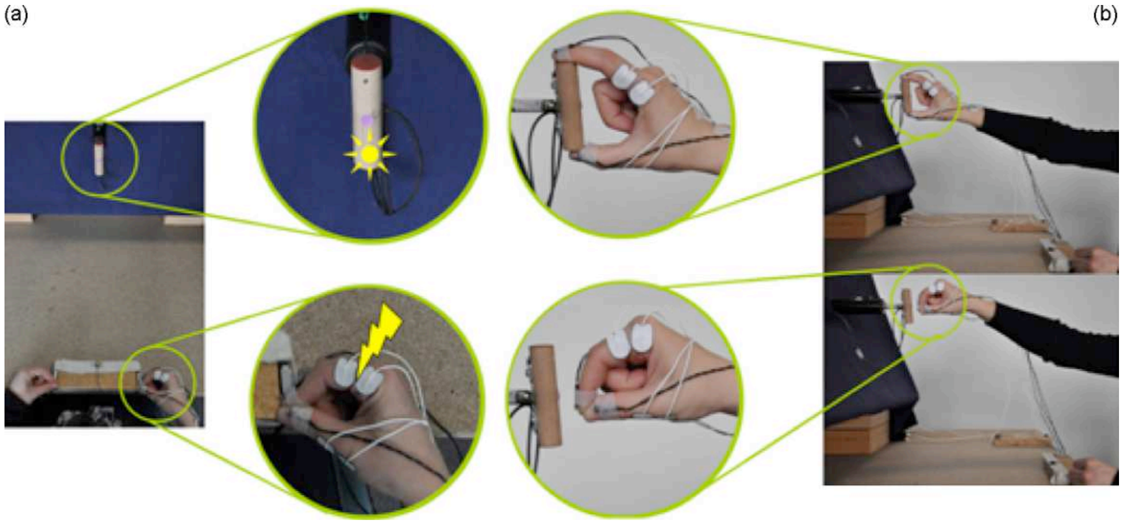

Fig. 1. Experimental setup and tasks. (a) Bird's eye view of the participant, sitting in front of the target cylinder (upper inset) with both hands in a pinch-grip starting position (lower inset) on a desk. The cylinder was positioned along the participant's mid-saggital plane, 47 cm away from hand's starting position. In the perceptual task, participants were asked to discriminate the elevation (i.e., up or down) of an electro-cutaneous target (yellow zap) delivered to the index finger (up) or thumb (down). A concurrent task-irrelevant visual distractor (yellow flash) could be presented from either the same (congruent) or different (incongruent) elevation (an incongruent instance is depicted in the insets), from one of two LEDs embedded into the cylinder extremities. (b) Participants were instructed to grasp the object with a precision grip (thumb-index, as shown in the upper inset) or to point to it (lower inset).

tem (Northern Digital Inc., sampling at 100 Hz, 0.01 mm 3D resolution at 2.25 m distance). The infra-red emissions were sampled at 100 Hz. Two infra-red emitting diodes (IRED) were stuck on the lateral part of the nail of the thumb and index fingers and one was placed on the interior part of the wrist at the styloid process level (Jeannerod, 1986). These markers were used to reconstruct the transport component of both actions (the change over time of the wrist marker position) and the grip component of the Grasping action (the change over time of the distance between the index and the thumb).

2.3. *Design and procedure*

Participants sat at a table in a quiet and dimly illuminated room, in front of the apparatus, with two response pedals under their right foot. They were instructed to maintain fixation on the black dot painted in the middle of the target cylinder. Participants performed two concurrent tasks during each trial: the perceptual task (speeded tactile discrimination) and the motor task. Across blocks, the motor task consisted in Grasping the cylinder along its longitudinal axis with the index and thumb (precision grip, Fig. 1b, upper circle) or Pointing the closed hand towards the centre of the cylinder longitudinal axis without opening the fingers (Fig. 1b, lower circle). In this latter condition, participants were instructed to stop the movement in close vicinity of the object but avoid contact with it. Each trial started with an auditory warning signal. After a variable delay (1500–2200 ms) a second auditory signal constituted the GO for the motor task. The motor task was performed using the stimulated right hand in both the Pointing and Grasping blocks. Regardless of which action had to be performed, visuo-tactile stimulation was unpredictably delivered between trials: (1) before movement start (Static condition) or (2) at the beginning of the movement (action Start condition) or (3) during the execution of the movement (action Execution condition). At the beginning of each trial the tip of the thumb and the index finger of each hand were kept in a closed pinch-grip posture on the start-switches. Start-switch release was used to trigger the visuo-tactile stimulation in the Start (0 ms) and Execution condition (with a 200 ms delay). Each trial was started manually by the experimenter concealed behind the apparatus, after the dowel had been rotated into one of the four possible orientations.

3. Results

3.1. *Multisensory remapping of space*

In a first ANOVA analysis, we contrasted all four factors: Action (Grasping vs. Pointing), Phase (Static vs. Start vs. Execution), Object Orientation (Anti-Clockwise vs. Clockwise) and Stimulation (Congruent vs. Incongruent). Briefly, we found a highly significant main effect of Stimulation [$F(1,15) = 15.57$, $p < .001$], confirming the presence of the typical cross-modal congruency effect (CCE, see Brozzoli et al., 2009; Spence, Pavani, & Driver, 2004; Spence, Pavani, Maravita, et al., 2004): participants proved faster in responding to congruent (420 ms) than incongruent (469 ms) trials, with a similar pattern of results also for the accuracy score [95% for congruent vs. 85% for incongruent trials, $F(1,15) = 17.61$, $p < .001$]. Hereafter, the dependent variable will thus be the CCE, calculated as the performance difference between incongruent and congruent trials, in that it quantifies the strength of the interaction between visual and tactile inputs. Unless otherwise specified, CCE will refer to the performance difference in terms of response times, which typically proved more sensitive in this type of experimental paradigms. However, we also examined the accuracy CCE (i.e., accuracy difference between congruent and incongruent trials) to exclude any speed-accuracy trade-offs. As a consequence, the following analyses only included Action (Grasping vs. Pointing), Phase (Static vs. Start vs. Execution) and Object Orientation (Anti-Clockwise vs. Clockwise) as variables.

A significant main effect of Phase [$F(2,30) = 16.18$, $p < .0001$] showed the dependence of CCE on the phase of the action in which subjects received the visuo-tactile stimulation. As Fig. 2 (upper panel) shows, an increase of the CCE was observed as soon as the stimulated hand started the action: the CCE was stronger when visuo-tactile stimuli were delivered at action Start (55 ms) than in the Static condition (26 ms; $p < .001$, Newman–Keuls post hoc test). The increase of CCE was also observed during the execution phase of the action (66 ms; $p < .001$ with respect to the Static condition). The same effect was present in the accuracy CCE [$F(2,30) = 4.43$, $p < .05$]; 6% for the Static condition, 7% for the Start ($p = .05$ with respect to Static) and 9% for the Execution ($p < .05$ with respect to Static). Critically, the effect of the Phase was differently modulated as a function of the action that participants were performing, as witnessed by the significant Phase X Action interaction [$F(2,30) = 6.19$, $p < .01$] in the CCE (Fig. 2, upper panel). In the Grasping condition, the CCE increased significantly in the Start (55 ms) with respect to the Static condition (22 ms, $p < .001$); and increased even further in the execution phase (79 ms, $p < .001$ with respect to Static and $p < .01$ with respect to Start condition). In the Pointing condition, the CCE was similarly increased in the Start (56 ms) with respect to the Static condition (29 ms, $p < .01$), but no further increase was observed during the execution phase (53 ms, $p < .01$ only with respect to Static condition, see Fig. 2, upper panel). Finally, a direct comparison between the two types of action showed a signifi-

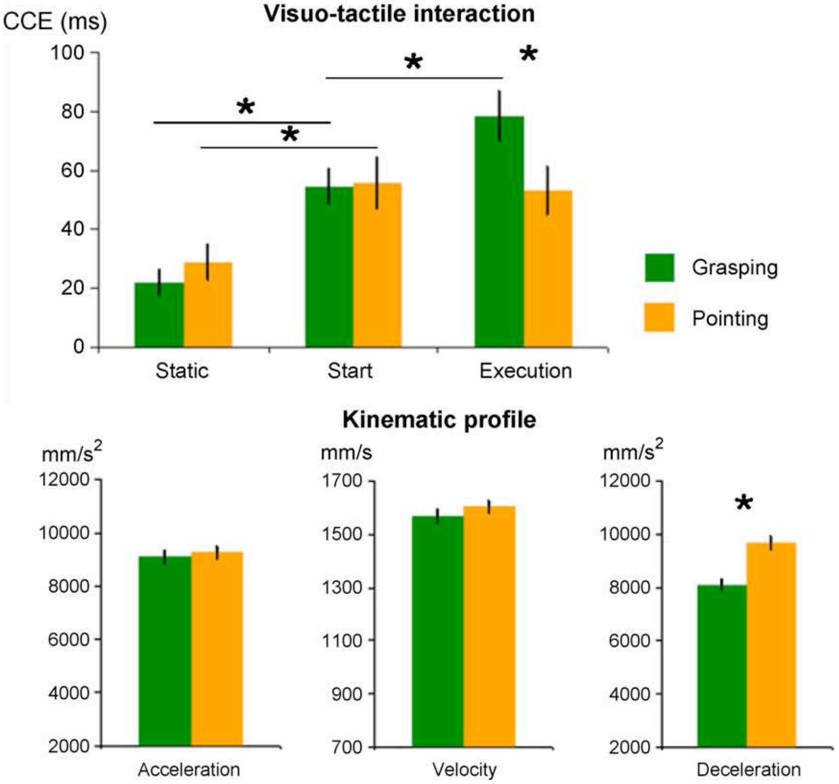

Fig. 2. Action-specific remapping of visuo-tactile interaction. (Upper panel) Means and standard errors are shown for the amplitude of the CCE as function of action phase. (Lower panel) Means and standard errors of the parameters of the reaching component for both actions: peaks of Acceleration (left part), Velocity (central part) and Deceleration (right part).

cant difference in the level of CCE in the execution phase, with stronger visuo-tactile interactions for the Grasping (79 ms) than the Pointing action (53 ms, $p < .01$). The post hoc comparisons did not present any other significant difference between Grasping and Pointing, in the amount of the CCE in Static (22 and 29 ms, respectively, for Grasping and Pointing, $p = .32$) and Start (55 and 56 ms, respectively, $p = .89$). A separate ANOVA performed only on Static and Start conditions confirmed this finding, revealing a significant effect of the Phase [$F(1,15) = 15.65$, $p < .01$] but no interaction with the type of action [$F(1,15) = 0.56$, $p = .46$]. When analysed in terms of accuracy CCE the interaction between Phase X Action was not significant, however a similar numerical trend was nonetheless evident excluding any speed-accuracy trade-off in the interpretation of the RT CCE results.

3.2. Differences in kinematics between Grasping and Pointing

Separate analyses were conducted on the kinematic parameters of reach-to-grasp and Pointing movements recorded in 3D space throughout the study. This served the important purpose of assessing any possible parallel between the motor and the perceptual performance (see Fig. 3 for a representative example from the Execution condition of one participant), in addition to documenting the difference between the two types of action. The following kinematic parameters of the movement were analysed: Acceleration, Velocity, Deceleration Peaks and relative latencies since movement onset, Movement reaction time and Duration (up to the closing of the fingers on the object to be then extracted from its support to complete the required action). Each parameter was entered in an ANOVA with the following independent variables: Action (Grasping vs. Pointing), Phase (Static vs. Start vs. Execution), Object Orientation (Anti-Clockwise vs. Clockwise) and Stimulation (Congruent vs. Incongruent).

As expected, the two actions differed in the ending part of the reaching phase. As shown in Fig. 2 (lower panel), the deceleration peak was influenced by the kind of action as a main effect [$F(1,15) = 14.72$, $p < .01$]: when participants pointed to the object, their deceleration was more important ($9668\,\mathrm{mm/s^2}$) than when

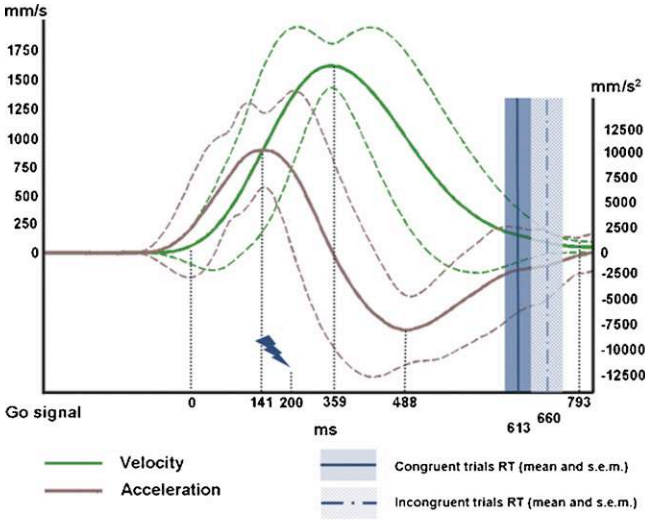

Fig. 3. Temporal coupling of perceptual and motor task. The graph illustrates the time-line of a representative Execution condition of one participant. Mean Velocity (green) and Acceleration (grey) profiles are plotted in the graph as bold lines, with 2 standard deviations intervals indicated by dashed lines. Interleaved with the kinematic profile, the blue zap indicates when during the kinematics the visuo-tactile stimulation occurred. Means and standard errors of Reaction Times for Congruent (full blue vertical line) and Incongruent (dashed blue vertical line) stimulations are also plotted.

they had to grasp it (8104 mm/s^2). No modulation was observed for the Velocity and Acceleration Peaks of both Grasping and Pointing movements. The latencies of these kinematic peaks were only partially modulated by the different kinds of actions to be performed. Indeed, the kind of action impacted only on the Latency of Deceleration Peak, which occurred later in case of Pointing (434 ms) than in case of Grasping (424 ms) in all experimental conditions ($p < .05$ in all comparisons) with only two exceptions, where the same non-significant trend was present (movements towards anti-clockwise tilted object in the Start condition and movements toward clockwise tilted object in the Execution condition).

3.3. *Influence of the perceptual task on kinematics*

Movement kinematics was partially affected by the different temporal coupling between the motor task and visuo-tactile stimulation. The incongruent trials presented delayed latencies of Acceleration, Velocity and Deceleration Peaks when stimulation occurred in Static (145, 310 and 434 ms, respectively, for the three parameters) rather than Start (136, 305 and 423 ms, $p < .05$) or Execution (136, 304 and 428 ms, $p < .05$) conditions. This is witnessed by the significant Phase X Stimulation interactions for Acceleration [$F(2,30) = 4.04$, $p < .05$], Velocity [$F(2,30) = 7.00$, $p < .01$] and Deceleration [$F(2,30) = 7.14$, $p < .01$]. These modulations were present regardless of which action was performed, Grasping or Pointing. Among the peaks, only the Acceleration Peak showed to be marginally modulated by the stimulation [Phase X Stimulation interaction, $F(2,30) = 4.45$, $p < .05$]: in case of congruent trials, Acceleration Peak resulted more important when stimulation occurred before (Static condition, 9411 mm/s^2) than on (Start condition, 9059 mm/s^2, $p < .05$) or after (Execution condition, 9101 mm/s^2, $p = .055$) the movement onset. Again, this effect was present both in case of Grasping and Pointing movements. No modulation was present for Velocity and Deceleration Peak as a function of the Stimulation. Finally, neither movement time nor motor reaction times resulted affected by the perceptual task (Table 1).

4. Discussion

In a recent study we showed that, when performing an action, our brain updates the relationship between distal visual input and tactile information at the acting hand well before the hand contacts with the object (Brozzoli et al., 2009). This perceptual re-weighting occurs already at the very early stages of the action, when the hand has barely moved from its starting position. Furthermore, it is updated continuously as the action unfolds. This finding showed for the first time that the brain can update the interaction between initially separated visual and somatosensory inputs, as a function of the sensori–motor transformations required by the action itself and suggested a functional link between visuo-tactile peripersonal space and voluntary actions.

4.1. *Action-specific remapping of peripersonal space*

In the present study, we took one step forward and contrasted the effects of two different actions, Grasping and Pointing, on visual–tactile interaction to assess any specificity in the modulation of peripersonal space as a function of the required action. For both actions, the interaction between task-irrelevant visual information on the target object and the tactile information delivered on the acting hand increased already at action start, thus providing further support to our original observation (Brozzoli et al., 2009). However, a different updating of the visuo-tactile interplay took place during the execution phase of the two different actions. While in the Grasping action the magnitude of the CCE was further increased during the execution phase, in the Pointing action the visuo-tactile interaction did not present any further increase during execution with respect to movement onset. In other words, during the actual approaching phase of the movement, Grasping triggered stronger visual–tactile interaction than Pointing.

This finding adds to our previous results by revealing not only that a continuous updating of peripersonal space occurs during action execution, but also that this remapping varies with the characteristics of a given motor act. If (part of) the remap-

Table 1
Means and standard errors for motor reaction time (ms) from the go signal, duration (ms) of movements and absolute reaction time (ms) to the perceptual visuo-tactile task in all experimental conditions.

		Inward				Outward			
		C		*I*		*C*		*I*	
Motor onset (mean ms, s.e.m.)									
	Before	346	21	375	21	340	17	347	18
Grasping	Start	395	24	387	18	384	20	402	19
	Execution	389	20	398	27	394	18	389	20
	Before	381	24	396	17	377	20	402	22
Pointing	Start	398	22	383	18	397	21	377	20
	Execution	392	22	380	19	395	21	399	26
Duration (mean ms, s.e.m.)									
	Before	686	24	703	20	718	18	722	19
Grasping	Start	724	25	707	27	723	18	725	19
	Execution	731	24	728	24	733	21	743	18
	Before	702	18	701	20	702	21	711	20
Pointing	Start	717	23	725	25	723	28	726	25
	Execution	733	24	726	22	722	31	728	25
Visuo-tactile RTs (mean ms, s.e.m.)									
	Before	419	19	444	27	413	20	431	23
Grasping	Start	463	24	516	32	453	23	509	32
	Execution	401	18	478	31	403	18	483	30
	Before	428	19	456	27	425	20	455	27
Pointing	Start	438	21	500	31	435	24	484	30
	Execution	384	15	427	28	377	19	440	27

ping of peripersonal space is already effective at the onset of the motor program, the perceptual modulation can be either further enhanced in case of relatively complex object-oriented actions like Grasping, or kept unchanged in case of simpler Pointing actions. This on-line, motor-evoked “monitoring” of the action space opens the possibility of very fast modulations of the peripersonal space representation as a function of more ecological needs during actions execution. One could speculate that such rapid on-line updating, for instance, could parallel the fast, on-line motor corrections documented in motor control studies (Desmurget et al., 1999; Farnè et al., 2003; Paulignan, MacKenzie, Marteniuk, & Jeannerod, 1991; Pisella et al., 2000). Since deficits of the so-called “automatic pilot” (Pisella et al., 2000) have been documented after lesions o the posterior parietal cortex in humans, as well as in healthy subjects after parietal TMS (Desmurget et al., 1999), one could suggest that the mechanism underlying the rapid remapping of peripersonal space could be damaged in these patients, thus depriving them from the “monitoring” of the action space. Ongoing research in our laboratory will help clarifying this hypothesis.

4.2. Peripersonal space remapping is selectively modified by specific kinematic patterns

The second main finding of the present study is that the kinematic results appeared remarkably associated with the perceptual modifications. We directly compared the transport component of the Pointing and Grasping actions. The overall kinematic structure of either Pointing or Grasping was not disrupted by the concurrent perceptual task. Whenever the tactile task affected some movement parameters both types of movement were affected similarly, thus showing that the visuo-tactile task did not differentially affected the kinematic pattern of Pointing and Grasping actions. Crucially, however, the opposite was not true, in that different kinematic patterns between Pointing and Grasping had a clear impact on the visuo-tactile task, which we used as a proxy of peripersonal space remapping. The only substantial difference appeared towards the end of the reaching component of the movement, during the deceleration phase. Namely, when subjects pointed towards the object, they needed to decelerate more than when they grasped it. This difference reflects the need for the subject to stop the movement before the collision with the object, with respect to the Grasping, where deceleration is weaker due to the need of achieving a stable grip when the fingers contact the target. It is to worth noting the parallel between the kinematic evolution of the two actions and the perceptual modulation of the visuo-tactile interaction. When the visuo-tactile interplay was assessed in the phase of the movement that did not present kinematic differences between Pointing and Grasping (i.e., start phase), a similar remapping of peripersonal space was found across the two different actions. By contrast, when the visuo-tactile interaction was assessed in the execution phase, i.e., when Pointing and Grasping differ from a kinematic point of view, the peripersonal space was also differently remapped. This parallel between the perceptual and the motor behaviour strengthens our proposal of a link between multisensory peripersonal space representation and the execution of voluntary actions. Moreover, the kinematic results allow us ruling out the possibility that peripersonal space remapping might be induced by the relative approaching velocity of hand and object. Indeed, the visual receptive fields of monkeys' bimodal neurons have been shown to present dynamic modifications depending on the velocity of an object approaching the corresponding tactile receptive field on the body (Fogassi et al., 1996). Thus, it would in principle be possible that the different increase of visuo-tactile interaction observed as a function of the required action might reflect differences in hand velocity between types of movement. However, no significant difference was observed between Grasping and Pointing velocities, with instead a tendency for the peak to be higher in the Pointing with respect to the Grasping action. If the perceptual remapping reported here were due to on the object's approaching velocity, we should expect higher visuo-tactile interactions in case of Pointing rather than in the Grasping. Instead, the opposite was observed, clearly supporting the notion that the remapping of peripersonal space we reported in this study is induced by the execution of a voluntary action towards the object and can be modified on-line as a function of the action requirements.

This functional role is not (see Brozzoli et al., 2009) in contrast with the view that peripersonal multisensory space serves involuntary defensive re-actions in response to objects approaching the body (Graziano & Cooke, 2006; Graziano & Gross, 1995; Makin et al., 2009). However, here we considerably add to this view by showing that in humans such multisensori–motor interfaces may be functionally involved in voluntary control of actions that bring the body towards objects. In particular, the present findings show a specific sensitivity of the peripersonal space to the kind of sensory–motor transformation that is required to execute an action. This fits well with the functional properties of visuo-tactile neurons documented in parieto-frontal circuits in the monkey, which code for peripersonal space. These neurons present spatially organised visual and tactile receptive fields (Avillac, Denève, Olivier, Pouget, & Duhamel, 2005; Duhamel et al., 1998; Fogassi et al., 1996; Graziano, 1999; Graziano & Gross, 1995; Rizzolatti et al., 1981, 1997) allowing this bimodal circuitry to represent an object in a coordinate system centred on the body and to be continuously updated during bodily movements. Indeed, some bimodal neurons also respond when the arm is voluntarily moved within the reaching space (Fattori, Kutz, Breveglieri, Marzocchi, & Galletti, 2005; Galletti et al., 2003; Gardner et al., 2007; Gentilucci, Fogassi, Luppino, Matelli, & Camarda, 1988; Marzocchi, Breveglieri, Galletti, & Fattori, 2008) and have been previously proposed to code goal-directed actions (Gentilucci et al., 1988; Rizzolatti et al., 1981, 1997). Neurophysiological studies in monkeys have additionally shown activation in the posterior parietal cortex during a Grasping movement, in the early phase of the action, when the hand has not yet reached the object. This activation gradually shifts towards the somatosensory cortex when the hand enters in contact with the object (Gardner et al., 2007). The on-line enlargement of the visual receptive fields of bimodal neurons in response to approaching objects (Graziano & Gross, 1995) or tool-use (Berti & Frassinetti, 2000; Bonifazi, Farnè, Rinaldesi, & Làdavas, 2007; Farnè, Bonifazi & Làdavas, 2005; Farnè, Iriki & Làdavas, 2005; Farnè, Serino & Làdavas, 2005; Holmes & Spence, 2004; Iriki, Tanaka, & Iwamura, 1996; Maravita, Spence, & Driver, 2003) converge in supporting the involvement of the bimodal system in the updating of the peripersonal space representation in dynamic conditions.

In conclusion, this study provides evidence that voluntarily acting on objects triggers specific remapping of multisensory perception as a function of action requirements, as specified possibly by the motor complexity alone, or its coupling with spatial information about the target object. Future studies will ascertain whether such a remapping mainly depends upon intrinsic (vs. extrinsic) properties, or reach-to-grasp (vs. reach only) components of movement. Most important at this stage is the fact that by showing that such a remapping is similar when action starts, but differs according to the differential kinematics of Grasping and Pointing during execution, we additionally demonstrate that action-dependent remapping of space is regulated in real-time and linked to the kinematic characteristics of the action. The multisensory-motor neural machinery acting as an anticipatory interface between the body and nearby events may thus have been selected throughout evolution to drive voluntary approaching movements via a continuous monitoring of action space.

Acknowledgements

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Discussion

The three contributions presented here addressed the issue of the need of an operational definition of the Body Schema, as well as the possibility to separate the concept of BS from the one of Peripersonal Space.

In the first paper, I proposed that the BS is an action oriented, plastic and internally coherent representation of the body. The two experimental contributions (Brozzoli, Cardinali, et al. 2009; Brozzoli, Pavani, et al. 2009) clearly showed that two out of three of these characteristics are present in the PpS.

Results of the first study speak in favor of a remapping of the spatial representation when a grasping movement is performed. This remapping consists of a higher level or stronger interaction between the tactile information on the hand and the visual one on the target object. Interestingly, this remapping is present already at the onset of the action and increases along the movement toward the target object, thus suggesting that the PpS is, as the BS, an action devoted representation. Moreover, this plasticity is not only functional to action performance but it is also modulated by which type of interaction with the object is implied by the action.

The second study indeed showed that the plasticity of the PpS depends on the kind of sensori-motor transformations required by the action. The comparison between grasping-dependent and pointing-dependent modulations of the PPS showed that, despite a comparable CCE at the beginning of the action was present in both cases, when the two actions started to differ one from another (as shown by the kinematic profile), so did the CCE.

Despite the similarities, it is reasonable to think that these two representations exist independently. As proposed in the review, physical contiguity between the body and the tool could be the key aspect, as tool-use it is not required to induce plasticity of the PpS (Brozzoli, Cardinali, et al. 2009; Brozzoli, Pavani, et al. 2009), while we will show that an actual modification of the body, or of the afferent information from its extremities, is necessary for inducing changes in the BS.

The aim of my thesis has been to test and describe the plasticity of the BS in healthy subjects. To do that, I needed an effective paradigm that allowed me to alter the current estate of the body to study the effect that this alteration may have on the representation of the body itself, and a measure suitable to detect the plasticity.

This paradigm is tool-use. This choice has been dictated by many reasons, among which, the importance of tools in humans' culture and daily-life activities, as well as the extraordinary skillfulness with tools our species has reached during evolution. The reasons of this choice will be further discussed in chapter 3, where I will also propose a brief review of some of the most relevant tool-use studies in humans.

Regarding the measure, I used, as main instrument, the kinematic approach. This approach allows one describing the motor behavior of subjects in terms of temporal and spatial parameters. Indeed, it derives directly from the definition of the BS as an action devoted representation of the body that a suitable way to test this representation is to study action, and in particular the way body-parts are moved. Basic principles of kinematics are the object of chapter 4 (p. 71).

Tool-use

What a tool is and what can it tell us about the BS

The ability to use tools is one of the most remarkable skills of the human species. It is so well developed that it is actually debated the issue of whether it has to be considered a peculiar and unique feature of the human kind, or if it pertains to other species too. Many studies have indeed reported observations of tool-use in animals, in the wild as well as in captivity. It is not the goal of the present chapter to solve this interesting issue. Here, I want to introduce tool-use as a suitable paradigm to induce changes in body configuration and thus study the plasticity of the body representation for action.

The choice of using a tool-use paradigm is grounded on a particular definition of what tool-use is and what is not. In particular, we refer to the definition given by Beck in 1980 and we lay down three conditions that have to be respected. In the first place, we consider tool-use as the use of an unattached external object; secondly, the object has to be used with a functional purpose that can, however, be different from the one the tool has been built for. Finally, we consider tool-use only the condition of actual utilization of the external object, and not for example the fact of simply holding it.

In the following review, all these aspects of tool use are discussed together with previous studies that implied tool-use as a paradigm to investigate the effect on space representations in healthy participants and patients. The review also points out an important aspect that has been already mentioned in the chapter 2. In particular, the fact that plastic changes of the Peripersonal Space has often been interpreted as plasticity of the BS.

11

Human Tool Use

A Causal Role in Plasticity of Bodily and Spatial Representations

Lucilla Cardinali, Claudio Brozzoli, Francesca Frassinetti, Alice C. Roy, and Alessandro Farnè

1. Introduction

Along the evolutionary history, humans have reached a high level of sophistication in the way they interact with the environment. As humans, we are able to modify, adapt, and shape the world around us according to our needs. One important step in this process has been the introduction of tools enabling humans to go beyond the boundaries of their physical possibilities. If it's true that we share tool use abilities with several other species like non-human primates (Peeters et al., 2009; Povinelli et al., 2010), birds (Weir et al., 2002), and rodents (Bird & Emery, 2009; Emery & Clayton, 2009; Okanoya et al., 2008), in humans this capacity is uniquely developed (Johnson-Frey, 2003). Ontogenetically, not only are we able to skillfully use tools that we know how to build, but we can also use tools we can't build or even invent: Not all of us know how to make a fork or a pen, despite the fact that these are among the simplest tools we use without any effort in our everyday life. The acquisition of tool use abilities is of great importance as it multiplies the ways we can interact with the external word. One obvious consequence is that the large use of instruments makes our relation with the environment mediated and less direct, a characteristic that can be comparable to the effect produced by using language. Moreover, if in animals the construction and use of instruments is related (and quite exclusively tested) in a context of problem-solving, human beings are the only species in which cultural components have deeply infiltrated tool construction, tool use, and even social desirability of tool use. In most Western cultures, for example, we can accept that a baby eats with her hands, but can't accept the same from an older child and surely not from an adult. The result of most of the tools we use is to separate ourselves from Nature, i.e., very different from animal tool use. Behind the complex phenomenon of phylogenetic development of tool use and its potential causal implication for higher forms of cognition, there are important "lower level" aspects of cognition that highlight how tool use plays a causal role in shaping both spatial and bodily representations, and this is the focus of the present chapter. First, we will offer a definition of tool and in particular of what can be called tool use in our perspective, for operational purposes. Second, we will focus on the causal role that tool use plays in producing changes on space perception and body representation. Third, we will discuss the challenges tool use presents for the sensorimotor system of the human and non-human primate brain.

2. What a tool is?

We can generally define a tool as an object used to perform an action, or more precisely as "the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool" (Beck, 1980). This somewhat classical definition illustrates several aspects that are necessary to make a clear distinction between what can, and should be, considered of as tool use and what cannot and should not be considered as such.

The first feature is that an object, to be considered of as a tool, must *actively* participate in the bodily movement. In this respect, a watch, even if it is in direct contact with a body part performing an action (e.g., the arm grasping an object), is not a tool in a proper sense. Thus, the passive contact with the acting body part is not a sufficient condition. Moreover, objects are not necessarily tools by the functional property derived from their original conception. A fork, for example, may be thought of as a tool because through it we can interact with another object, producing a modification in the environmental state of that object (e.g., picking up some food and move it to the mouth). In other words, a fork has been built to be a tool that directly modifies the status and/or position of an object in the environment. However, we could label the use of the fork as tool use when, being in the same lunch type of situation, we use the fork to point to a person that just came into the restaurant we are having lunch in with a friend. This function is not the one the fork has been created for, but it is still a voluntary goal-directed movement with the specific aim of changing the environmental status of an object. Here, the object may be our friends' attention to be drawn to the direction pointed to by the fork. In contrast, in our perspective we cannot talk of tool use when, during the same lunch situation, we are just holding the fork or moving it in the air and gesturing with it during the conversation. Such an action makes the fork devoid of both its original conceptualization as a tool and the possible new function of drawing somebody else's attention somewhere. In our view, the mere presence and/or the aimless use of a tool are not sufficient conditions to allow talking about tool use. Still, it might be debatable whether using a fork to shift somebody's attention somewhere in the environment (i.e., object-mediated deictic pointing) fully meets the criteria to be properly considered of as tool use.

Here we propose a definition of tool use as a purposeful goal-directed use of an object to sensibly interact and modify the environment that adheres quite substantially to the definition proposed by Beck; We are tool users *when* we (are about to) use a tool (not simply hold one) with a particular aim, no matter if it's the one the tool is built for (contextual functionality). In this respect, it has been recently demonstrated that the monkey brain itself is able to disentangle between moving a tool and using a tool. Umiltà and colleagues (2008) recorded neurons from sub-regions of the premotor and motor cortices (areas F5 and F1) of two macaque monkeys while using normal or reversed pliers to grasp food. They found that neuronal activity in F5 and F1g (a further subdivision of F1; see for details Umiltà et al., 2008) was related to the different phases of a grasping motor act. Interestingly, careful examination of their tapes and the activity of the neurons reveal that while the monkeys were simply opening and closing the tool *between* trials, no activity was detected in the very same neurons that fired vigorously when a opening and closing action was purposely performed *within* a given trial to grasp food. Therefore, moving pliers does not necessarily entitle such movement as tool use, as in one case (inter-trial opening–closing movements) it may merely represent a sort of filler, or appetitive behavior. These observations, besides strengthening the idea of a goal-centered organization of the motor cortex, clearly fit with our proposed definition of tool use.

As the body has often been described as the interface between the brain and the external world, a tool can be added to this chain in a position between the body and the environment. From this perspective, we now turn to examine the body and space as those representational levels that are at either end of a tool, starting from the distal ring of the chain (see Figure 11.1), the external space.

3. Modifying the external space with tools

Tools allow us to act on the external space, possibly by producing a modification in a way that would not be possible without the tool, or in a sector of space that would not be otherwise accessible. This latter is the case for many tool use studies.

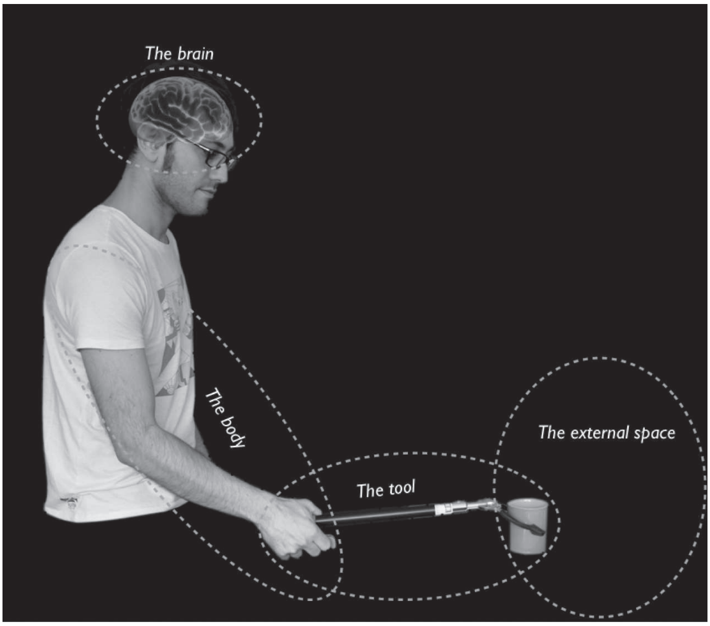

Figure 11.1 The body has been described as the interface between the brain and the external space. In this perspective, tools can be considered as an intermediate ring of this chain. Because of their special position between the body and the external space, they might produce modifications in both domains.

For example, in a classical tool use paradigm, subjects are requested to use a rake to retrieve distant objects—objects that are too far away from the subject to be retrieved with the hand alone without implying some whole body displacements, or locomotion. We know from neurophysiological, behavioral, and neuropsychological literature (Brozzoli et al. 2006; Cardinali et al., 2009a; Farnè et al., 2005b; Graziano & Gross 1995; Rizzolatti et al. 1998) that "space" is not represented as a unique map of the external world; different spatial regions can be defined, mainly on the basis of the kind of interaction we can have with each sector of space. We can indeed distinguish a far extrapersonal space, where object manipulation is not possible without locomotion; a reaching or near space, defined as the space where an object can be reached with the hand without further movements of the trunk; a peripersonal space, as a particular region of space around body parts and, finally, a personal space, which is the space occupied by the body (see Cardinali et al., 2009a for discussion on the relationships among these representations).

Tool use changes space perception

Previous studies have shown that the boundaries between the different sectors of space are not rigid, nor sharply defined. In this respect, tool use has been applied extensively as an interesting and successful paradigm to reveal and quantify such a new conception of plasticity of the margins between different regions of space. This has been particularly related to those tools that allow subjects to act in far, non-reachable space. As a paradigmatic example, Berti and Frassinetti (2000) showed that the definition of far and near space may clearly depend upon the action possibilities available to the tool user (see also Gallese & Sinigaglia, 2010; Legrand et al., 2007). They investigated a right-brain-damaged patient affected by a pathology known as left spatial neglect (neglect, hereinafter), who showed to be affected by neglect symptoms selectively in the reaching, but not in the far extrapersonal space. Visual neglect is classically tested with paper and pencil tests, among which the line bisection task is a most typical one: the patient is presented with a horizontal line in front of her and asked to mark a vertical sign on the middle of the line (i.e., to bisect it). In most neglect patients the sign is markedly deviated to the right, ipsilesional side. In their original contribution, Berti and Frassinetti (2000) asked the patient to bisect also lines located far away from the subject's body, by using either a long wooden stick or a laser pointer. Remarkably, the patient showed neglect not only for the close lines, but also for the lines located in the far extrapersonal (i.e., preserved) space. Critically, this pathological performance was observed only when the patient bisected distant lines with the stick, but not when using the laser pointer. Interestingly, despite the fact that the stick and the laser were used to the same aim (i.e., bisect the line), they did not have the same effect on space representation. This difference was explained by the authors by advancing that the laser does not change the spatial relationships between body and external objects, whereas the stick does. The authors interpreted this effect as a consequence of a remapping of the far extrapersonal space as near space.

A complementary pattern of results has been reported by Ackroyd and colleagues (2002) who studied a patient with neglect affecting selectively the far extrapersonal space (i.e., the opposite dissociation with respect to the patient reported above). They asked the patient to use a long stick to point toward objects and observed a better performance for objects located in the neglected part of the space when using the stick than when using the hand alone. Therefore, these provide convergent, although opposite, support to the conclusion that using a tool may "displace" the boundary of the space around us.

Similar findings have been reported in neurological patients affected by clinical extinction, a pathological sign somewhat related to neglect (Brozzoli et al., 2006; Làdavas & Farnè, 2004). Typically, extinction patients are able to report a tactile stimulation on the contralesional hand when it is presented alone, but fail to report the same stimulation when it is delivered at the same time with an ipsilesional one. This phenomenon has been largely documented to occur also when the tactile contralesional stimulus is delivered concurrently with a visual stimulus on the ipsilateral side (cross-modal extinction, see di Pellegrino et al., 1997). Crucially, the visual stimulation needs to be located in the peripersonal space, i.e., close to the patient's hand, to be effective in extinguishing the tactile one. By testing a group of patients with tactile extinction, Farnè and Làdavas (2000) provided evidence of remapping of peripersonal space via tool use. They hypothesized that, if the peripersonal space undergoes a remapping due to the use of a tool extending the reachable space, after tool use a visual stimulus located far from the patient's ipsilesional hand should enter the peripersonal space representation and thus be able to extinguish the contralesional tactile stimulus. Accordingly, they assessed visual–tactile extinction before, immediately after, and 10 minutes after patients were engaged in a brief training with using a rake to retrieve distant objects. As predicted, cross-modal extinction was more severe after tool use, even if the visual stimulus was at the same (far) distance from the patient's hand. In the light of this finding and by analogy with the neurophysiological data (e.g., Iriki et al., 1996) they suggested that tool use would "expand" the peri-hand space, a spatial metaphor to convey the notion that tool use increases the multisensory weights assigned to the processing of a visual stimulus in a given (far) position.

This idea has been supported since by several studies on both neurological patients and neurologically healthy subjects. In most of the studies on healthy subjects, the so-called cross-modal congruency effect (CCE, Spence et al., 2004) has been used as a proxy for cross-modal, visual–tactile extinction. In a nutshell, the CCE paradigm provides a measure of the interference a visual stimulus (distractor) can exert on the subject's performance (either reaction time or accuracy, or both) in discriminating a tactile (target) stimulus. The CCE therefore provides a quantitative behavioral measure of the strength of the interaction between vision and touch. Quite remarkably, such a measure has been shown to vary as a function of the distance between visual distractors and the tactile targets delivered on the subject's hands, similar to visual–tactile extinction. Owing to such a spatial selective feature, the CCE has been extensively used to test the strength of visual–tactile interaction in the peripersonal space and has confirmed that the use of different types of tools can rapidly modulate the expression of CCE. In particular, after tool use an increase of CCE can be observed at relatively far locations from the subject's body (Farnè et al. 2007; Holmes et al., 2004, 2007a, b; Maravita et al., 2002).

Conditions for tool use to remap space

Once again, it seems that as tools allow us to act in different spaces and, in some way, to be present in a far extrapersonal space, they also make the brain to compute this space as if it were closer. The crucial aspect of such a remapping of space seems to be attributable to performing an action. Only when actively using a tool one can observe this kind of plastic changes (Maravita et al., 2001, Farnè et al., 2005a). More precisely, it is only the movement that pertains to the functional part of the tool that is taken into account during spatial remapping as, for example, the modification of peripersonal space occurs selectively with respect to the functional—and not the physical—length of the tool (Farnè et al., 2005c; Bonifazi et al., 2007). The simple presence of an instrument in a hand is not sufficient per se to induce such changes, and we can have clear intuitions of this characteristic as being an evolutionary advantage. In a natural context, our visual scene is not "clean" as in a laboratory context. We often see many objects concurrently, thus many potential tools. Let's think to the example we opened the chapter with. If you are seated in a restaurant having lunch with your friends, you will probably have many (real and potential) tools close by (forks, knives, spoons, etc., for each person seated at the table), but you will use only a few of them and not always the same. So the brain needs to distinguish what is useful for incorporating and what is not. Action seems to be the criterion to do this (Maravita et al., 2001, Farnè et al., 2003, Farnè et al., 2005a). It seems therefore clear that performing actions shapes space representations and these and other findings from the tool use literature suggest that when an action is executed with a tool, the change the tool brings about in the movement has also a consequence in the representation of space even *before* the actual use of the tool. Witt and colleagues (2005), for example, showed that the mere intention to use a tool to perform an action is sufficient to modify the representation of the reaching space. These authors asked healthy subjects to estimate the distance of a visual target before reaching it with or without a stick. Participants judged the target to be closer when the subsequent movement had to be performed with the stick, as compared to the condition in which they had to use their hand. In a control experiment with no action involved, but only target estimation, the presence of the tool did not affect the perceptual judgment, thus clearly indicating that the intention to use the tool, and the planning of the subsequent action, were responsible for the modification of the way in which the reaching space was perceived.

Switching from near to far space

Recently, Longo and Lourenco (2006) investigated the relation between near and far space in neurotypical individuals to test whether there is a sudden switch, or rather a graded transition without sharp interruption, from one to the other. They additionally verified whether and how tool use would affect such a boundary. To these aims, they asked subjects to bisect lines located frontally at different distances (30, 60, 90, 120 cm) from their body, with a laser pointer or a stick. They found that when asked to bisect lines in the near space (within reach) with a laser pointer, subjects showed a small but significant bias to the left, a phenomenon commonly known as pseudo-neglect (Bowers & Heilman, 1980; Jewell & McCourt, 2000). With increasing distances, this bias gradually shifted to the right irrespective of the extent of arm's reach, suggesting continuity instead of an abrupt shift between the representations of the two regions of space. Moreover, in a subsequent work (Longo & Lourenco, 2007), the same authors found a relationship between the subjects' arm length and the extent of the bias. In particular, subjects with a longer arm showed a more gradual shift in bias with increasing distance when compared to those with shorter arms. Interestingly, and in agreement with the neuropsychological results reported above, when subjects were performing the same task with a stick, the leftward bias persisted even for the farthest distance, in line with a tool-mediated remapping of the far as near space. These findings proved resistant to changes in the visual context, as they have been replicated in a study where subjects acted in a virtual reality context (Gamberini et al., 2008).

Spatial remapping: is the presence of a tool necessary?

Despite their diversity of approaches, the studies reported in the previous sections clearly converge, indicating that the active use of a tool is necessary for remapping space. What these studies do not tell us, however, is whether the joint presence of these elements (an action and a tool) is necessary for such spatial changes to occur. In other words, owing to the link between action and space representations, action could be the crucial feature to induce spatial remapping, while the fact that action is exerted via a tool might be a subsidiary aspect of space remapping. The tight link between action and space is also reflected in a partial overlap in the use of two fundamental concepts: the peripersonal space and the body schema. These two representations, related respectively to space and action, have a common history and they have often been considered, and used, as interchangeable concepts. A reason for this confusion to persist so long in the literature is that both peripersonal space and body schema have been often studied via tool use paradigms. We recently addressed the question of whether peripersonal space and body schema can be considered as two separated concepts (Cardinali et al., 2009a). Of particular interest here, we asked whether the above reviewed changes in peripersonal space perception could be similarly obtained when an action is performed without any tool.

More specifically, we tested the role of the visual–tactile interaction, occurring in the peripersonal space, in the control of voluntary, free-hand actions. The hypothesis is that, the hand-centered representation of peripersonal space could be useful for guiding the hand toward targets. By referring to a neurophysiologically identified network of cerebral structures that represents peripersonal space in the animal on the basis of multisensory processing (Fogassi et al., 1996; Graziano & Gross, 1995; Rizzolatti et al., 1981a–c), Brozzoli and colleagues (2009a, p. 917) precisely suggested that "the multisensory-motor neural machinery represented by this network might have been selected throughout evolution not only to drive involuntary avoiding reactions, but also voluntary approaching movements toward objects, via continuous monitoring of action space (i.e., the space within reach)." Using the CCE paradigm described above, Brozzoli and colleagues asked subjects to discriminate a tactile stimulus delivered on the right hand (up-down discrimination) while ignoring a visual distractor presented far from the hand on the object that had to be grasped. The perceptual task was presented at different timings: before the hand started moving, at movement onset, or during the early phase of the execution of the grasping movement. The results showed an effect of action onset and execution on the CCE, in the form of a greater interference that was exerted by the visual distractor on the tactile task. Such an increased interference appeared as soon as the hand started to move (as compared to the CCE observed before movement onset) and was further enhanced during action execution (Brozzoli et al., 2009). These findings provide evidence that remapping of peripersonal space was induced by the free-hand grasping action. In other words, one may metaphorically propose that when an object must be grasped, it "enters" the peripersonal space region since the very beginning of the action. This tool-independent modification of the peripersonal space suggests that peripersonal space and body schema, despite their close relation, could be considered as separated representations, although both are sensitive to tool use manipulations. To date, there is no definitive evidence (yet) that tool use-dependent effects on peripersonal space do not also affect the body schema, or vice versa. All together, however, these findings show that in free action, peripersonal space can be changed without the need of using tools, thus possibly not implying changes in body schema. In tool use, by contrast, the tool becomes incorporated in the body schema, and, most likely, changes in peripersonal space also occur. Thus, evidence suggest that action per se might be a necessary and sufficient condition for spatial changes to occur, whereas the mere presence of a tool is neither necessary (Brozzoli et al., 2009, 2010) nor sufficient (Farnè et al., 2005a; Holmes et al., 2004, 2007a, b; Maravita et al., 2002).

4. Modifying the bodily representation with tools

In the previous section we reviewed the findings that have been shown so far on the effects of tool use on space representations. Different paradigms involving tool use have revealed how planning and executing an action in far space make this space to be represented as nearer. Moreover, visual–tactile interaction in the peripersonal space varies as a consequence of both tool use and free-hand actions. We have underlined how all these effects are thus related to action and in this section we focus on the challenges our sensorimotor system must deal with while controlling a tool for its use. We will also discuss what the consequences deriving from tool use are for bodily representations, instead of spatial ones.

Effects of tool use on the sensorimotor system

Following the chain schematically presented in Figure 11.1, we now proceed from the external space to consider the brain representation of the body as the agent of tool use. The first stop is at the level of the tool–hand interaction. Tactile perception and discrimination abilities at the hand are particularly developed, these features being functionally rooted in the highest density of somatosensory receptive fields, at the periphery, and in cortical magnification at more central level. We saw in the previous section that tactile information on the hand is strongly linked to visual information near the hand and that this interaction contributes to forming the peripersonal space. Peripersonal space can be metaphorically thought to "enlarge" to encompass a used tool and thus producing space remapping. However, when we use a tool to act upon an object, we cannot directly touch the object, although we get visual feedback about the contact of the tool on the object. What we feel, then, comes from the hand, but the source of this sensation comes from the far end of the tool. How is this potential conflict solved?

Yamamoto and Kitazawa (2001) showed that when we feel tactile inputs on the hand via a hand-held tool, the tactile information is referred to the tip of the tool itself. These authors asked neurotypical participants to perform a temporal order judgment (TOJ) task that consisted in judging which of two tactile stimulations was delivered first.

Stimuli were presented at the tip of a hand-held stick in four different conditions. Hand and tool straight ahead, hand-crossed with tool-uncrossed, hands and tools crossed, hand-uncrossed with tool-crossed (see Figure 11.2). This kind of TOJ task is known to be influenced by hand posture; in particular, one can usually observe a reversal in the pattern of performance when the hands are crossed at the subjects' midline (i.e., the left hand located in the right hemispace, and vice versa). Interestingly, the authors found the same pattern of reversal in performance under the condition when tools, but not hands, were crossed. Moreover, under the condition where both hands and tools were crossed, the subjects' performance was exactly the same as under the hands and tools straight ahead condition (Figure 11.2), clearly showing that the tactile stimulation physically perceived by the mechanoreceptors of the hand skin was referred to the tip of the tools. This finding has been replicated by the same group in a virtual reality context (Moizumi et al., 2007). In the latter study, subjects were holding a stylus in each hand and they had visual and force feedbacks about the position of the tip of the tools that were presented on a screen. The task was the same as in the previous experiment, judging which of two tactile stimuli came first, but the conditions were different. Subjects were tested in two possible hand positions (crossed and uncrossed) and received force feedback in such a way as to create the feeling of crossed or uncrossed hand, independent of the actual hand posture. Similarly to the previous study, they found an inversion of the performance pattern when the force feedback signaled that tools, but not the hands, were crossed. What is of particular interest in this study is the fact that it is the force feedback, more than the visual one, which is responsible for the referral of tactile stimuli to the tip of the tool. Once again, it is the action-related information that determines the effect of the tool.

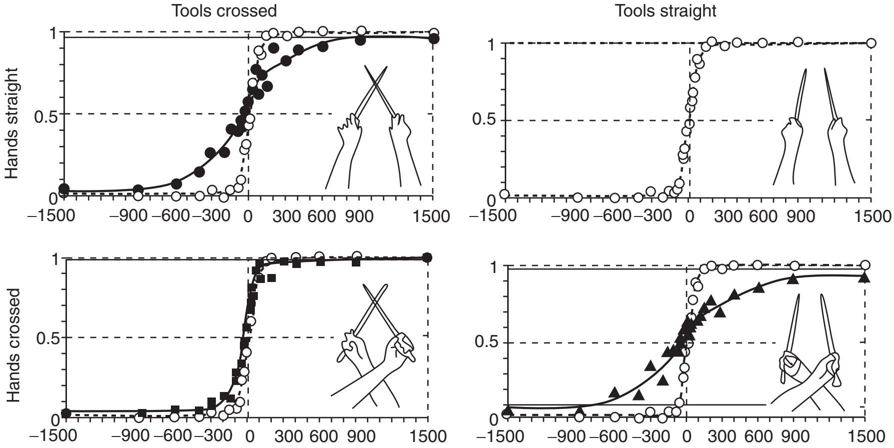

Figure 11.2 Temporal order judgment of two tactile stimuli delivered at the tip of drumsticks under four different conditions: hands straight (upper panels)/crossed (lower panels) and sticks straight (left column)/crossed (right column). In each graph the probability of the stick in the right hand to be stimulated earlier (y axis) is plotted against the different stimulus onset asynchrony, SOA (x axis). Data for the straight hand/straight sticks (upper right panel) are superimposed in all the other graphs. Modified from Yamamoto & Kitazawa (2001).

A similar aspect is to be considered for the motor control of the tool. When we write with a pen, for example, the consequences of our movements and the associated goal are achieved by the pen, despite the motor control exerted by the brain on our hand. At the same time, the attentional focus is not on the hand, but on the tip of the pen (Holmes et al., 2004). Recently, Müsseler and colleagues (2009) addressed the question of what is perceived of the hand movement when we are using a tool. They asked a group of neurotypical subjects to track a circular moving target presented on a display by moving a stylus on a digitizer tablet. The gain for the *x*-axis and the *y*-axis between the display and the tablet was manipulated so that subjects had to draw an ellipse in order to track the target moving in a circle and they were also asked to judge whether they were tracing a vertical or a horizontal ellipse. The results showed that participants were extremely uncertain about their hand movements, as shown by the threshold value at which they were able to judge their performance. In a second series of experiments, the authors additionally manipulated the amount of visual feedback provided to subjects to examine whether the presence of the cursor on the screen would influence the ability to evaluate hand movements while drawing circles. They found performance was even worse without visual feedback, suggesting that tactile and proprioceptive information were too poor to correctly estimate the trajectories traveled by the stylus. The important conclusion is that in tool use the motor control, similar to that shown for the tactile perception, is referred to the tool itself. From a functional point of view, and by virtue of its role in object interaction, the tool can be seen as a substitution of the hand or the arm.

It is indeed impressive how precise human beings are in using tools and even in switching from using one tool to another. Again referring to the daily life situation with which we opened this chapter, during a dinner we constantly switch from free-hand movements (grasping a glass to drink) to tool use (picking up the food with a fork) and from one tool (the fork) to another (a knife). How does this happen? The answer is likely to be found in the brain's highly plastic abilities and in particular in the process of incorporating a tool in the representation of our acting body, i.e., the body schema.

Incorporation of the tool

The body schema is an action-oriented body representation used for planning and executing body movements, and it is thought to be dynamically shaped by actions (Head & Holmes, 1911; Schwoebel & Coslett, 2005; Sirigu et al., 1991). It is outside the scope of this chapter to extensively treat the body schema matter and the debate that currently exists about its precise definition and role, together with the existence of (how many) other bodily representations (see, for review, de Vignemont, 2005; Longo et al., 2010). Here, for sake of clarity, we will always refer to the body schema as the representation the human brain relies upon to plan and execute bodily actions (see, for details, Cardinali et al., 2009a). By definition, thus, the body schema contains information about the spatial position and size of the body and its parts. Indeed, it is the knowledge of our body parts position in the space and of their dimension that constitute crucial information to correctly perform an action. When we want to grasp an object, we need to know where is the hand we want to use, its distance from the target object, how long is the arm, etc. All this information is supposed to converge on the body schema representation,

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and they also change in time: we constantly move our body so the position of its parts needs to be updated after each movement and even online, during movement execution.

Our body changes also in dimension and shape across life: these changes must also be taken into account by our body schema. Interestingly, size and position changes typically occur within very different time scales (very fast for the latter, much slower for the former), except in the case of tool use. In fact, as soon as we grasp a tool to use it, we increase our body dimensions quite dramatically, although temporarily. The time-scale problem in the motor control of tools has recently been addressed by Kluzik and colleagues (2008). Despite the possible different perspective regarding tool use definition and properties in Kluzik and co-workers' study (e.g., the tool was a manipulandum inserted in a force field, thus not fitting our definition of tool), we consider their study interesting because the authors measured the adaptation to a force generated by a robot controlling the manipulandum (eventually controlled by the subjects' hand), as well as the after-effects induced on free-hand movements, under different conditions. In particular, after the learning period, subjects were divided into two groups: the first group performed a "free-space" session immediately after learning (free hands reaching without holding the robot), followed by a second learning session and finally a "force null" session, during which they had to move the arm while holding the manipulandum that no longer applied any force. The inverse sequence (learning-"force-null"-learning2-"free-space") was used for the second group. They found that *motor learning* induced by controlling a handle that was submitted to viscous force fields and consisting of a new mapping between desired action goal and force applied to achieve it transferred only partially to free-hand reaching movements. What is of particular interest to us here is the difference between gradual and abrupt introduction of the force field. The group who was assigned to the gradual condition, in which the force perturbation was introduced gradually during the training phase, showed a much greater learning of the internal model of the arm than the other group, in which the force field was introduced abruptly, so that the force perturbation was maximal since the first training movement. This suggests that the temporal information is informative for the brain and used to distinguish the origins of two, only apparently, similar processes. The brain appears to be able to make the distinction between gradual and abrupt changes and to ascribe the first to arm-related modifications and the latter likely to tool characteristics (Kording et al., 2007).

Detection of time-scale differences in movement execution could be a cue for the brain to optimally adapt motor control. However, as we said earlier, tool use introduces an abrupt modification in what is normally changed on a much larger time scale: body size. It has already been shown that relatively rapid changes in morphology, as those induced in achondroplastic dwarfs submitted to elongation of lower limbs through the Ilizarov technique, produce a cortical reorganization in the somatosensory cortex (di Russo et al., 2006). In a series of behavioral experiments, we recently demonstrated that even more rapid, though less dramatic, changes in body dimension can be taken into account by the body schema (Cardinali et al., 2009b). In particular, we tested the effect of using a 40-cm-long mechanical grabber for a few minutes.

As illustrated in Figure 11.3, we asked healthy participants to perform free-hand movements (grasping an object and pointing on the top of the same object) before and after a period of training with the tool, which consisted in grasping the same object, but with a 40-cm-long mechanical grabber. We recorded subjects' kinematics to compare

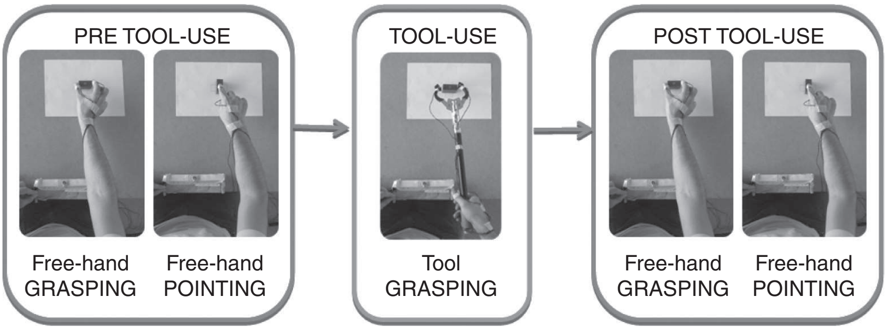

Figure 11.3 Experimental time course. In the pre-training phase (left) subjects were asked to perform reach-to-grasp and reach-to-point movements, in separated blocks, toward a differently oriented object. Training (center) consisted in performing reach-to-grasp movement toward the same object with the tool. Post-training phase (right) was identical to the pre-training. Reprinted from *Current Biology,* **19**(12), Lucilla Cardinali, Francesca Frassinetti, Claudio Brozzoli, Christian Urquizar, Alice C. Roy, and Alessandro Farnè, Tool-use induces morphological updating of the body schema, pp. R478-R479, © 2009 with permission from Elsevier.

the free-hand grasping movements performed before and after tool use. When analyzing the parameters of the transport phase of the grasping movement (i.e., the phase during which the hand travels toward the object) we found that subjects reached the maximum of movement velocity and deceleration later compared to actions performed before tool use. In addition, the maxima values, including those for acceleration, velocity, and deceleration, were significantly lower in amplitude (see Figure 11.4). Finally, the total movement time was longer, compared to before tool use. Noteworthy, no changes were observed for the grasping phase of the movement.

This pattern of results means that the same free-hand movement was performed in a different way by subjects selectively after having used the tool. Indeed, changes in kinematics may reflect a change in either the perception or action domain. However, were the tool use effects to be exerted over perception (instead of action), the kinematic changes would have been different. For example, if subjects perceived the distance between the target object and their hand as being shorter (instead of their arm as longer), the latency of the kinematic pattern would also be slowed, but the amplitude of these same parameters would have been increased (i.e., opposite to the observed decrease illustrated in Figure 11.4). Therefore, the tool use-dependent changes are more appropriately ascribed to changes in the sensorimotor than in the perceptual domain. Interestingly, the very same pattern of kinematic modifications was present also for the free-hand movement that was not trained with the tool, the pointing task. This additional finding suggests that what was modified by tool use was the representation of the arm itself, and that this change can be generalized to other movements, provided they contain similar transport components.

An interesting point needs to be discussed with respect to the previously reported Kuzlik et al's study (2008) and related ones, proving the existence of motor after-effects following learning to counteract force fields applied to manipulanda (frequently considered within this literature as being a sort of tool). Those studies (e.g., Malfait et al.,2002; Mattar & Ostry, 2007) provided clear evidence for the role played by motor learning on kinematics of subsequent movements, and some also showed that after-effects following

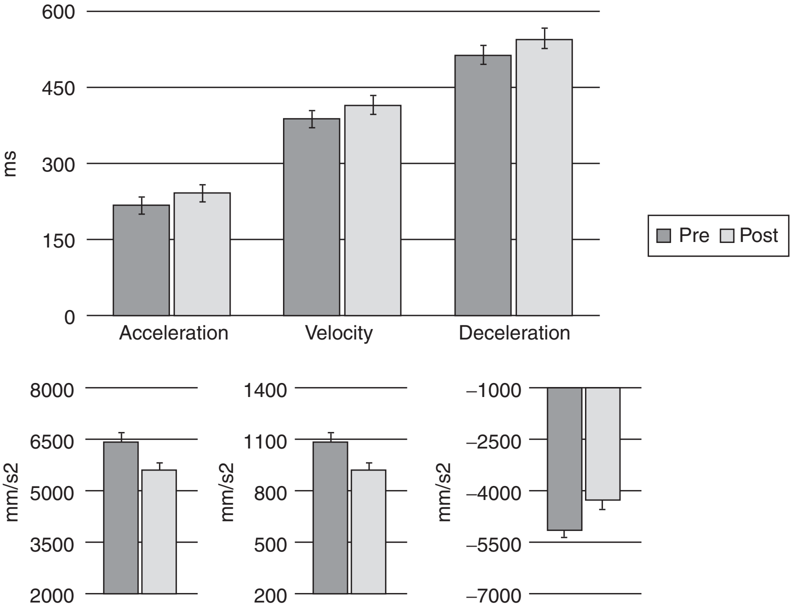

Figure 11.4 Kinematics results for the pre-training versus post-training comparison of reach-to-grasp movements. After the use of the mechanical grab, subjects showed longer latencies (upper panel) and reduced peaks amplitude (lower panel) for most of the parameters of the transport component. Bar graphs illustrate mean values for each parameter ± SEM. Reprinted from *Current Biology,* **19**(12), Lucilla Cardinali, Francesca Frassinetti, Claudio Brozzoli, Christian Urquizar, Alice C. Roy, and Alessandro Farnè, Tool-use induces morphological updating of the body schema, pp. R478-R479, © 2009 with permission from Elsevier.

motor learning may also affect sensory aspects (Mattar & Ostry, 2007). These sensorimotor after-effects, however, cannot be selectively attributed to tool use, or exclusively to a change in bodily representations. At odds with previously reported motor after-effects, in fact, our recent work showed effects on both motor kinematics and somatosensory aspects following tool use (see below) that were completely independent of motor learning. When the kinematics of the tool use training phase was analyzed, we indeed observed no signs of motor learning. No change was present when comparing kinematics of the very first tenth of trials, executed by subjects with the tool, and the last tenth of trials, thus proving that our "reach-to-grasp with the grabber" task did not imply any kind of motor learning or adaptation. This was true despite subjects not being familiar with this kind of grabber. It thus seems clear that, besides being overall more ecological, our tool use task that directly derives from the operational definition of tool use offered at the beginning of this chapter is quite different from learning the use of a manipulandum in the classical force-field approaches (Shadmehr & Mussa-Ivaldi, 1994). Owing to the documented absence of learning processes, the effects we observed on the kinematics of free-hand movements and on the perceptual task after using the mechanical grabber cannot be interpreted as an after-effect due to a motor-learning process.

Furthermore, we introduced a critical control that assessed for a possible role of muscle fatigue. The same free-hand movements (grasping and pointing) were recorded and compared in a novel group after the same amount of training that, however, did not imply the use of the grabber. In this control experiment, an extra weight was wrapped around the participants' wrist. In this case, as for the tool use training, subjects had an object added to their arm with a weight comparable to the weight of the tool (300 g), but the object was not a tool as it was not actively involved in the reach-to-grasp action. Under such a control condition, the results revealed no modification in the kinematic pattern of movement performed after the training with the wrapped weight, thus confirming that tool use induces selective modifications on the arm representation the brain uses to plan and execute actions.

Another interesting finding from this study was that the post tool use modifications nicely parallel the morphological differences in the subjects' arm length that are naturally present between subjects, i.e., whether they have short or long arms. Indeed, analyzing our subjects' kinematics we discovered that subjects with a longer arm tend to show longer latencies, reduced peaks amplitude, and longer movement times than subjects with a shorter arm. This pattern is comparable to that found when comparing free-hand movement after tool use with those recorded before tool use. This parallel clearly suggests that the representation of the arm length is the variable that is modified by the use of a long tool, and in particular the modification consists in a longer representation of the arm.

In order to directly support this claim, and provide independent evidence in support of the hypothesis that tool use modifies the body schema, we asked subjects to perform a somatosensory localization task before and after tool use (Cardinali et al.,2009b). Subjects were blindfolded and required to point to each of three possible tactually stimulated locations (middle finger tip, wrist, elbow) on their right (tool-trained) arm before and after the use of the grabber. We found that, when a given tactile spot was stimulated and subjects were asked to point to it, they actually pointed to a different place after tool use.

As illustrated in Figure 11.5, the mean distance between the spots subjects pointed to was more important after the use of the tool than before, as if subjects pointed to an elongated arm. This was true despite the fact that the arm location and posture adopted during this somatosensory localization task were different with respect to those adopted during the tool use training, ruling out possible alternative explanations in terms of the tool inducing changes in space, instead of arm representation.

To conclude, these findings clearly showed that tools are integrated in the representation of the body parts the brain uses to perform actions. We would like to speculate here that this is because we are able to use tools in such a skilful way, as if, one would say, they were our own arm.

5. Conclusion

In this chapter, we reviewed some of the most seminal works on tool use, from the perspective of the causal role played by tool use to shape, and possibly generate, relatively low-level features of spatial and bodily cognition. These studies clarify that what we consider to be a normal and simple activity of our daily life is actually the result of a complex series of processes that take place in our brain. Using a tool representsa great challenge for our sensorimotor system, as it involves modifications of body and space representation

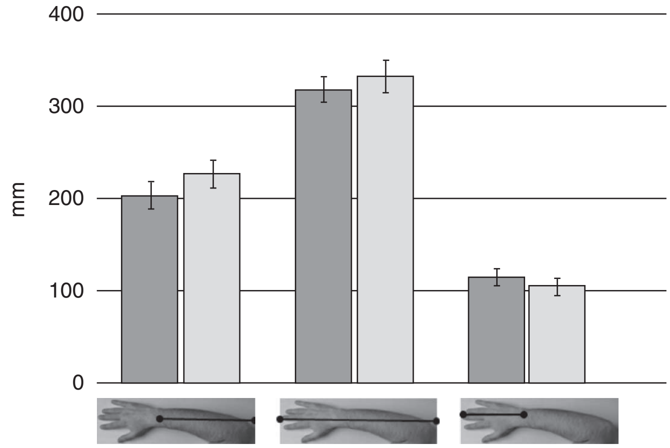

Figure 11.5 Results for the pointing localization task before and after tool use. Bar graphs show mean distance (± SEM) between the tactually stimulated anatomical landmarks (showed in the pictures) as estimated by the subjects. A significant effect was found for the distance elbow–fingertip that is mainly to ascribe to the elongation in the estimation of the wrist–elbow segment. Reprinted from *Current Biology,* **19**(12), Lucilla Cardinali, Francesca Frassinetti, Claudio Brozzoli, Christian Urquizar, Alice C. Roy, and Alessandro Farnè, Tool-use induces morphological updating of the body schema, pp. R478-R479, © 2009 with permission from Elsevier.

that are dynamically shaped by the movements we make with (and without) the tool. Although situated at a relatively low level of cognition, we believe that the sensorimotor changes produced by tool use may share some basic rules with higher cognitive functions. In this context, we would like to speculate that causation may move from basic principles embedded in unconscious processing (e.g., tool use increases the represented arm's length) to more sophisticated and "thinkable" ones (e.g., "to get that apple before me, I need a longer tool than what I have in my hand now"), possibly leading to a progressively increased sophistication not only in the use, but also in the construction of tools. When compared to the time scale of the evolutionary history, human tool use is a skill that appeared relatively late. Human beings had to wait to obtain a certain brain volume and characteristics before being able to produce, what we consider now to be, rudimental tools some 2.5 million years ago. Moreover, the evolution of this set of skills took a long time as, some authors claim, it only prospered starting from the so-called "human revolution" around 40,000 years ago (Corballis, 2003; Mellars, 1989). It is therefore reasonable to speculate that higher forms of causal cognition have evolved along with an increase in brain volume and in motor skills, to end up emancipating causality from materialistic contexts. Together with language, tool use is one of the greatest evolutionary conquests for the human species, probably responsible for our survival so far.

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Discussion

In the present review, we proposed to precisely adhere to the definition of tool-use originally advanced by Beck (B. Beck 1980). This definition underlies all my experimental work. The advantage of a tool-use paradigm is the possibility to induce fast changes in body morphology, so that the plasticity of the body representation can be studied in a laboratory context. It is true that other paradigms allow producing changes in body configuration. We already discussed in the previous chapter the use of the RHI. However, we saw that this particular paradigm is more likely to modify the BI. Since tools are objects used to perform actions, their incorporation is more likely to involve the body representation for action. In my thesis I provide evidence in favor of a specific effect of tool-use on the BS and not on the BI (see study 2).

It is also true that, in daily life, body configuration and size can be modified by many others factors, such as growth, injuries, amputations etc. These sources of modifications differ in terms of time scale, as well as for the type of reorganization they imply in the sensorimotor system. We already mentioned in chapter 1 that the BS is not strictly a short-term representation, since different action related information can have different time scales. For example, changes in posture are faster and more frequent than changes in size that happen throughout life. At the same time, as in the case of tool-use, size update must be sometimes quick if a correct motor control has to be maintained. In the study n. 2 one aspect will be again discussed, that is the description of tool-use as the employment of an external unattached object. We formulated the hypothesis that the BS is able to disentangle between two different sources of body modification and in particular between tool-use and lengthening of body-parts (thumb and index finger, in the present case). As described in the review, the attribution problem has been already addressed by Kluzik and colleagues (Kluzik et al. 2008) using a force-field adaptation paradigm, thus in the context of motor learning. The authors found that, depending on the causal attribution of the perturbation, i.e. to the arm or to the manipulandum, the transfer of the adaptation varied. In our study, we showed that using a tool (“unattached external object”), or lengthening the fingers (by attaching wooden sticks) has different effects on the BS (see study 2).

Another main point raised by the review concerns the effect of tool-use on the representation of the Peripersonal Space. We discussed the issue of the relationship between Body Schema and Peripersonal Space in chapter 2. Here we review some of the most important works that support the notion that using a tool in the far extrapersonal space produces a remapping of this portion of space. In particular, by allowing action in a region of space that was inaccessible before, the tool induces a recoding of far space as near space. This has been shown through enlargement of visual receptive fields in monkeys' bimodal neurons (Iriki, Tanaka, and Iwamura 1996), changes in visuo-tactile integration in healthy subjects (Maravita, Spence, et al. 2002) and patients (Farnè, Iriki, and Làdavas 2005; Farnè and Làdavas 2000) and tool-use dependent biases in bisection in neglect patients (Berti and Frassinetti 2000). A key aspect, although of secondary importance in this chapter, arises from all these studies. Space representation depends on action possibilities: the representation of what is near (or far) is built on the fact that I can (or can not) act in that particular region of space. This action supremacy is of great importance: if we push the reasoning further we can readily realize that the decision about the possibility of acting on a particular region of space depends in turn on the knowledge about the size of the body that, in an action context, might be provided by the BS. Longo and Lourenco (2007) showed indeed that there is a relation between the arm size and the representation of the extent of the near space. A functional update of the BS can thus produce secondary effects not only on motor control, but also on space perception. For example, Witt and colleagues (Witt, Proffitt, and Epstein 2005) showed that when subjects are asked to use a tool to reach an object, they also estimate the same object as being closer to them compared to when they are not asked to subsequently act on the object with the tool.

In the last ten years, researchers started to investigate the neural basis of tool-use moving mainly from two fundamental questions. The first one arises from the observation that tool-use is a motor skill particularly developed in human beings, in such a way that for a long time it has been considered as uniquely present in our species (Oakley, 1956). Although we now know that we are not the only animals using and building tools (Visalberghi et al. 2005; Visalberghi et al. 2009; Povinelli, Reaux, and Frey 2009; Povinelli and Vonk 2003) differences exist in particular in the capacity of understanding the causal relationship between a tool and its effects. The first question is then whether this capacity is underpinned by a specific neural circuit, possibly of recent appearance in the evolution, which might be present only in humans. Peeters and colleagues (Peeters et al. 2009) made a comparative fMRI study where humans and monkeys (trained and untrained to tool-use) were presented with movies of hand actions and tool actions. They found a large overlapping circuit between humans and monkeys extending from occipitotemporal areas to the intraparietal sulcus (IPS) and ventral premotor cortex (vPM), activated for all the type of grasping. Interestingly, in humans, observation of tool grasping led to the activation of an additional area in the inferior parietal lobule (IPL), that is the anterior portion of the supramarginal gyrus (aSMG). This area plays a critical role in the storage and retrieval of learned movement representations associated with skilled actions (Heilman, Rothi, and Valenstein 1982; Poizner et al. 1998) and has been found activated in previous studies during preparation for and pantomimes of tool-use (Johnson-Frey et al, 2005; Moll et al, 2000; Rumiati et al, 2004), as well as by the sound of tools (Lewis et al. 2006). It has been proposed that the role of the aSMG in the tool-use network (including left inferior frontal, posterior parietal and posterior temporo-occipital areas) is to activate learned motor representations related to familiar tool-use (Valyear et al. 2011; Peeters, Simone, Nelissen, Fabbri Destro, et al. 2009), which would allow human beings to predict the functional consequences of using a tool.

The second question is whether grasping objects with a tool relays on the same well-established cortical network mediating hand grasping. It has been proposed that the tool-use cortical network includes frontal, parietal and temporal regions, as well as the cerebellum, that are strongly interconnected and differently participate in tool skills by dealing with different aspects of such a complicated behavior (Goldenberg and Spatt 2009; Imazu et al. 2007; Tsuda et al. 2009; Johnson-Frey 2004). Tsuda and colleagues (2009) found a consistent overlap between the hand-grasping related activations and tool-related activations. In a PET study they asked healthy subjects to pick-up small objects and place them in a basket either with their own dominant hand (precision grip involving the thumb and the index finger) or a pair of chopsticks. Both tasks, when compared with a rest condition, induced a large activation in the sensorimotor system (M1, SI, SII, PMd and PMv, SMA and cingulate cortex), parietal cortex (SPL, IPL, IPS and VIP), the middle temporal gyrus in the left hemisphere. PMd, SMA, SPL and the cingulate motor areas were also activated in the right hemisphere. However, grasping with tools induced a higher activity in SI, PMv (BA 6) and PMd, PPC, MT and the cerebellum in the left hemisphere, as well as the SPL bilaterally when compared to precision grip grasping with the hand. A recent study confirmed the involvement of the PMv, PMd and PPC (an and in particular of the SMG) in coding hand peripersonal space (Brozzoli et al. 2011). Tsuda et al's pattern of activation could then reflect the neural basis of peripersonal space plasticity induced by tool-use, which has been previously shown in neuropsychological and behavioral studies (Berti and Frassinetti 2000; Farnè, Iriki, and Làdavas 2005; Maravita, Clarke, et al. 2002; N. Holmes, Calvert, and Spence 2004). Activation of the middle temporal gyrus is compatible with retrieving of knowledge about the tool. The same area has been found activated by naming tasks selectively for tools (Chao, Haxby, and Martin 1999; Martin et al. 1996) as well as knowledge recalling about action associated with tools (Kellenbach, Brett, and Patterson 2003). An increase of activation for the tool-use condition compared to free-hand grasping was found in S1, and in particular in the inferior portion that usually represents face areas, although Faillenot and colleagues (Faillenot et al. 1997) found an activation in similar location for grasping of complex objects. Superior parietal activation is explained by the authors with the need of visuo-spatial attention due to the level of difficulty of the task. Finally, the cerebellar cortex activation is compatible with coordination of motor skills required by the use of the chopsticks. Imamizu and colleagues (Imamizu et al. 2000) asked healthy subjects to use a computer mouse to track a target in which the rotational transformation was modified. They showed a robust activation of the cerebellum at the beginning of the task. The activation was reduced and limited to a smaller portion of the cerebellar cortex at the end of the training, suggesting that the cerebellum is involved in learning new internal models of the tool.

Although the relevance of tool-use skills in everyday life and the importance of knowing its neural correlates, only very few imaging studies have been performed to date to investigate tool-use. In a recent review, Lewis (Lewis 2006) compared 64 different paradigms investigating the neural correlates of tool-use, among which only one (Inoue et al. 2001) consisted in actual tool-use. Up to know, together with Tsuda et al's and Imazu et al's (2007) studies, these are the only examples of imaging studies on real tool-use[7]. In the other cases, because of the well-known constraints imposed by fMRI technics on movement execution within the scanner, subjects were asked to either imagine, or pantomime the use of a tool. Although similarities exist between neural circuits recruited by performing action and motorically imagining to perform the same actions (Parsons 1987) it has been recently shown that pantomiming the use of a tool does not activate the same areas as the actual use of the same tool (Imazu et al, 2007). In the future, particular care should be taken when developing more natural and complex situations in which tool-use should be closer to real life activity. A first step in this direction has been made by Culham and colleagues (Culham et al. 2003; Cavina-Pratesi et al. 2010) who developed an innovative apparatus to study free-hand grasping movements with fMRI. Recently, they also tested subjects during a task of grasping with pliers (Gallivan, Cavina-Pratesi, and Culham 2009) to test which brain areas are involved in the representation of what is near (reachable) and what is far (not reachable). The results of this study will be discussed together with the results of my study 3.

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[7] In addition, it has to be noticed that all these studies were run on Japanese subjects using chopsticks, that is a very well known and used tool in that population. It means that they can not inform us about the problem solving as well as learning process related to tool-use. Also, the motor constraints imposed to the subjects were so heavy that only one out of these studies actually required movements of the arm (Tsuda et al, 2009). This situation is far from real life and has the risk of reducing one special feature of tool use, that is the possibility to overcome human body limitations by performing actions otherwise impossible.

Kinematics: revealing the brain's cognitive architecture by analyzing motor performance

The kinematic approach consists of describing movements in terms of spatial and temporal parameters, such as velocity, acceleration, path length, trajectory, movement time etc. However, its impact is not limited to the mere description of the displacement of a particular body part in space. Indeed, since the first kinematic study to the control of the hand (Jeannerod 1981), this approach has been used to investigate cognitive functions such as objects representation, space perception and social interaction. In my thesis work, I decided to use kinematic of free-hand and tool movements to access the Body Schema and its plasticity. The choice of this approach derives directly from the definition of the Body Schema as an action devoted representation. Indeed, if we suppose that the BS contains all the body-related information the brain needs to accurately guide action, a change in it would necessarily be reflected in the way the action is performed. Moreover, as I showed in the chapter 3, previous studies that addressed the issue of the effect of tool-use on the Body Schema, actually failed in giving a conclusive answer mainly because of the approach they used. Authors actually reported changes in either visual-tactile interaction near and far from the body, but not direct evidence for the effects on the body representation itself. In this chapter, I will describe a selection of the most influential works on the kinematics of grasping and pointing movements, as these are the types of movement I used in my experiments, and I will show that this approach is a powerful tool and a suitable one for studying the body representation for action.

Kinematic organization of a grasping movement

Research on the highly developed human grasping skills starts in the early 80's and since then a considerable amount of work has been published on the kinematics, as well as on the neural circuits underneath this ability.

We owe most part of our knowledge about motor organization of grasping movements to the work of Marc Jeannerod, who started the prolific series of studies on human kinematics. In 1981, Jeannerod and Biguer first described the kinematic profile of reach-to-grasp movements and proposed a theory about the organization of this movement, known as the "visuo-motor channels" theory. According to this theory, grasping movements are composed by two types of motor behavior, reaching and grasping. Each component is based on a visuo-motor channel that elaborates particular aspects of the target object as a function of the to-be-performed movement.

The reaching (or transport) phase consists of carrying the hand towards the object and is thus mainly represented by displacement of proximal joints of the arm. The object information relevant to this phase includes the position, orientation and distance in space, which are called "extrinsic properties" as they do not belong to the object per se and can vary for a given object in different moments. These properties are coded with respect to the body position and in particular to the effector (the hand) position.

The grasping (or grip) component is constituted by the movement of the fingers involved in the grasping and consists of the pre-shaping of the hand configuration during the approaching phase to the target object. This behavior is based on the so-called "intrinsic properties" of the target object, which include the size, shape, weight etc.

In terms of kinematic parameters, a normal grasping movement is characterized by a bell-shaped velocity profile, where the peak is reached at about the 40% of the entire movement time, which is usually defined as the time between a consistent increase in velocity and the moment when the fingers firmly contact the object. The part of the movement from the velocity peak to the end of the movement is called deceleration phase and is usually not longer than 1/3rd of the entire movement time (Jeannerod 1981; Jeannerod and Biguer 1989; Jeannerod 1984). Derived from the velocity is the acceleration profile that is characterized by an early positive peak (achieved before the velocity peak) and a late negative peak (the deceleration peak).

Soon after the movement start, the hand begins to shape according to the objects features. In the case of a precision grip, that is when the object is grasped between thumb and index, these two fingers, which are usually in contact in a standard starting position (i.e., pinch-grip), begin to move away one from the other until they reach a maximum distance, called maximal grip aperture (MGA). This happens at about 60-70% of the entire movement time. The MGA is precisely modulated by the size of the object to grasp, although it is always larger than the object itself. The relation between the MGA and the object size is constant and known, so that for an increase of 1 cm in object size, MGA will increase by about 0.77 cm (Marteniuk et al, 1990). Once the MGA reached, the fingers start to close until they touch the object. From the spatial profile of the thumb and index finger, another parameter can be derived, that is the velocity of fingers aperture in which two peaks can be observed. The first is a positive peak and appears just before the MGA; the second is negative and it signals the moment in which the fingers are closing faster. Studying the time at which this peak appears (its latency), Jeannerod (1981) observed a temporal coincidence with the deceleration peak. This means that the fingers close faster when the wrist is slowing down in its approach to the object suggesting the existence of a highly functional coupling between the transport and grip components of the movement.

Although the model postulates a relative independence of the two components, they are not considered as completely separated. Transport and grip components are indeed described as being functionally interrelated to subserve a common general goal, which is to achieve a stable grasp for holding and eventually manipulating the object.

To test the relation between the two components, researchers used many different paradigms based on the following rationale: if the two components are coded in separated visuo-motor channels that elaborate different object characteristics, namely the intrinsic and extrinsic properties of the object, then the variation of one of these properties should affect only the channel devoted to its processing, but not the other. For example, if the object position in space (extrinsic property) is coded as a function of the transport component, grasping the same target object, though located at different distances from the hand starting position, should affect the transport component, leaving the grip component unaltered.

I will now present studies that addressed this issue by varying different properties of the target object and then studying the effect on the kinematics profile of the movement.

Effect of extrinsic properties

The extrinsic proprieties of an object are mainly the position in space and the distance with respect to the body. By changing the distance between the body and the target object, the amplitude of the movement also increases. Several studies found that more important movement amplitude implies a higher velocity and acceleration peaks (Jeannerod 1984; Gentilucci et al. 1991; Gentilucci et al. 1992; Chieffi and Gentilucci 1993) and longer movement times. The increase in movement time, despite a higher velocity peak, has been interpreted as a lengthening of either the acceleration phase (Chieffi and Gentilucci, 1993), or the deceleration phase (Gentilucci et al., 1991). The object distance has been thus proved to affect the transport component of the movement. However, the same authors also found a modulation of the MGA as a function of the distance. In particular, Chieffi and Gentilucci (1993) found that MGA is larger for longer movements. This finding support a coordination between the two components of the grasping so that when the movement has greater amplitude and is thus longer, the MGA is also rescaled and appears later. This rescaling seems to be more likely due to the increase in movement velocity (Jakobson and Goodale 1991) rather than a general increase in movement time.

Effect of intrinsic properties

I already mentioned the linear relationship that has been observed between object size and MGA amplitude. It has also been observed that grasping a smaller object imply an anticipation of the MGA (Castiello et al, 1992; Chieffi and Gentilucci, 1993; Jackobson and Goodale, 1991) and a reduction of the velocity of fingers aperture. The anticipation of the MGA could be explained by considering the object's size in term of contact surface for the fingers (Bootsma et al. 1994). With the exception of Efron objects, typically, a small(er) object offers a small(er) contact surface, which is the space available for the fingers to grasp and hold the object. This is a constraint that increases the level of difficulty of the movement and it is therefore possible to read the anticipation of the MGA in terms of making a longer time available to close the fingers with the requested precision. This interpretation is compatible with the observation of effects of the object size on the movement time (longer for smaller object; Chieffi and Gentilucci, 1993; Castiello et al, 1993) and length of the deceleration phase. Again, it seems that a strong interconnection exists between the transport and grip component, although their independent existence is supported. The explanation proposed by Jeannerod (1995) is based upon the existence of a hierarchical organization. At one level, specific channels are activated to extract the relevant visual information about the object and planning the appropriate behavior. At a higher level, a mechanism that represents the internal model of the action exerts a top-down control on the channels. From this top-down control derives the synchronization between the two components in terms of starting, phasing at the end of the movement (as shown by the tight relation between deceleration peak of the wrist and the negative peak of the velocity of fingers aperture) and stopping (both components stop at the contact with the object). The principle that drives this coordination between transport and grip component is time-based, so that the total movement time is accorded to the component that needs it more and the other one will be slowed down (Jeannerod et al. 1995).

The study of movements' kinematics is a powerful and reliable approach that allows the description of human movements and is also sensitive to minor variations in the target's characteristics. In the context of this thesis work, I used kinematics to study changes in the motor control of the effector of the action. At the best of my knowledge, no kinematic experiment has been previously conducted to investigate the role of the effector properties, rather than those of the target properties, on action performance. However, it seems reasonable to hypothesize that grasping movements may reflect not only the properties of the object, but also the features of the effector used to perform the action.

Kinematics in practice

I mentioned above the kinematic parameters that are typically used to describe a movement. The present paragraph will briefly illustrate the steps I undertook in the process of the analysis of movement kinematics, from the movement acquisition to the movement description.

All the experiments that are described in the results section, have been performed at the “Mouvement et Handicap” Platform at the neurological hospital, in Bron. This platform is equipped with an Optotrak system (Optotrak 3020, Northern Digital Inc., Ontario, Canada), consisting of three infrared cameras recording at a frequency of 100Hz for the first study and 200Hz in the second and third studies.

To track the displacement of subjects’ arm and hand, custom-made infrared emitting diodes (IRED) are placed directly on the skin at specific positions. One is placed on the wrist, at the level of the styloid process, in order to extract information about the transport component of the movement. The other two IREDs are placed on the extremities of the finger involved in the movements, i.e. one on the medial lower corner of the thumb nail, one on the lateral lower corner of the index finger nail (study 1 and 3). For the study 3 an additional IRED was applied on the later low corner of the middle finger nail. Data from these markers provide information about the grip component of the movement.

Once the movement recorded, off-line analyses are performed using a Matlab-based software developed in the laboratory (Main). The curves of velocity and acceleration are calculated from the data of the IRED placed on the wrist (see Figure 10). The curve of velocity of fingers aperture and the spatial profile of the fingers are derived from the IRED of the thumb and opposing finger, i.e., either the index or the middle finger (see Figure 11).

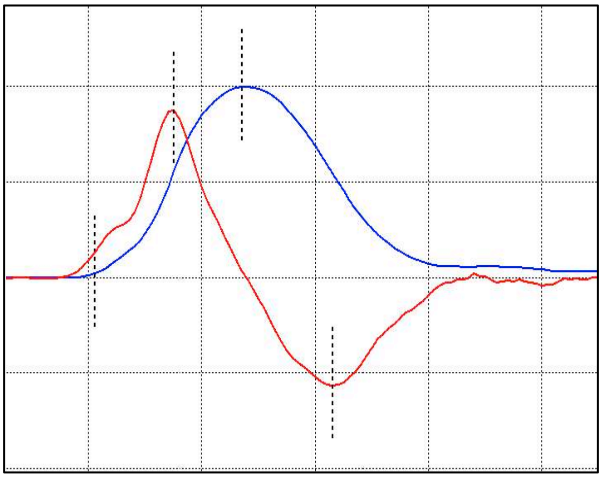

Figure 10. Example of the kinematic profile of the transport component of a free-hand grasping movement.
The Acceleration (RED line) and the Velocity (BLUE line) have been calculated on the wrist marker. Black bars indicate the detected onset time and peaks.

Peaks detection is done in a semi-automatic way by defining standard parameters. Movement onset is defined as the first point in time after a series of twenty consecutive frames in which the velocity is increasing. The movement end, for the grasping movements, is detected on the closure of the grip, i.e. on the fingers profile, as the first frame in time after a series of consecutive stable frames in position.

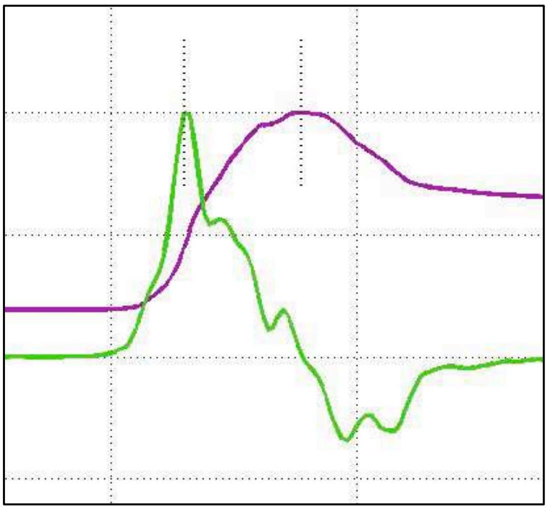

Figure 10. Example of the kinematic profile of the grip component of a free-hand grasping movement.
The Velocity of Grip Aperture (GREEN line) and the Grip Aperture (purple line) have been calculated on the thumb and index markers. Black bars indicate the detected peaks.

RESULTS

STUDY 1

Tool-use induces morphological updating of the body schema

Cardinali et al, Current Biology, 2009

The aim of the first study was to provide a direct evidence of the plasticity of the BS. The idea that the representation of the body for action is plastic is, as shown in the first chapter of this thesis, an old one. However, it remained an idea supported by converging, but indirect evidence. Theoretical arguments were in favour of this idea. In particular, the fact that a correct motor control, that is the main goal subserved by the BS, is based on a precise knowledge of the body state at a given time implies the necessity of a constant updating. Many sources of perturbation of the states of the body are possible. The human body changes in size throughout the entire life following timescales that vary across individuals and, for a same person, for different body parts. Even more frequent and brisk are changes in posture and relative position of body parts.

To make BS plasticity observable in a laboratory context, we chose a tool-use paradigm. Tool-use is indeed an important part of the human motor repertoire. Although subjects had no previous experience with the particular tool we asked them to use, we are all, as human beings, skilful tool-users. Moreover, tool-use has also a long history as an experimental paradigm, since it has been applied to the study of space representations in humans and animals.

Here, the reasoning was the following: the BS is the representation of the body used to plan and execute actions. During the use of a tool like the mechanical grab chosen for our experiments, the configuration of the acting limb (the right arm) is transiently modified. In order to maintain a good performance, the BS must integrate the characteristics of the tool in the arm representation; in other words, the BS has to incorporate the tool. If this is the case, we should be able to detect traces of this incorporation shortly after the end of the tool-use period. Kinematics, as fine-grained description of the motor behaviour of a subject, can be a suitable technique to detect this plastic update. If the representation of the arm is indeed modified, the action executed by the subject should be affected by the update and be thus different form the same action executed before the use of the tool.

We designed a series of experiments where healthy subjects were asked to perform free-hand grasping and pointing movements toward a target object before and after a period of tool-use. During this period, subjects used a 40-cm long grab to grasp a target object. In an additional experiment, the tool-use phase was substituted by an equivalently long phase of free-hand grasping movements where subjects were wearing a weight, matching the one of the tool, around their right wrist. This was done to control for any possible effect of muscle fatigue, as well as for the possibility that mere repetition of grasping movements might affect subsequent kinematics. Kinematic analyses were run on all the performed movements. Finally, we designed a task to indirectly derive the representation of the arm length through pointing movements: three different spot on the right arm of each subject were stimulated tactually and the task for the participants consisted of pointing with the left (untrained) hand toward the felt stimulation on the right (tool-trained) arm in order to localize it. Distances among the estimated position were then derived off-line and compared between pre- and post tool-use.

The kinematic analysis of the grasping and pointing movements performed before and after the tool-use phase, but not the weight phase, showed that subjects' movement profile was characterized by longer latencies and reduced peaks amplitudes for the transport component parameters. We interpreted this new kinematic profile as the trace of the update of the representation of the arm length in the BS due to the temporary incorporation of the tool. This interpretation was supported by the results from the tactile localisation task, where we found that after tool-use, the indirectly estimated distance between the elbow and fingertip was longer than before the use of the tool.

Correspondence

Tool-use induces morphological updating of the body schema

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To control bodily movements the human brain relies on a somatosensory representation referred to as the body schema [1]. The almost century-old hypothesis that tool-use induces plastic changes resulting in the tool being incorporated in the body schema is nowadays widely accepted. Whether this somatosensory representation is truly modified remains unknown, however, as tool-use has never been shown to affect arm motor behaviour. Here we report that using a mechanical grabber that physically extends the arm does alter the kinematics of subsequent free-hand grasping movements. Remarkably, tool-use after-effects generalise to pointing movements, despite the absence of specific tool-training. Furthermore, this effect is driven by an increase of the represented length of the arm: after tool-use, subjects localised touches delivered on the elbow and middle fingertip of their arm as if they were farther apart. These findings indicate that tool-use alters the body schema, and also show that what is modified is the somatosensory representation of intrinsic properties of the body morphology.

The body is not a constant object. The morphological changes it undergoes throughout life do not affect the brain's ability to accurately move limbs and grasp objects, the cerebral representation of our body-parts' dimensions and positions being constantly updated [2]. Plastic changes of the body schema have been advocated also to explain human and non-human skilful use of tools [3–6]. While tool-embodiment has been shown through perceptual changes in peripersonal space [7–9], cortical correlates of motor imagery and even time perception (see Supplemental references in the Supplemental data available online), there is no evidence that tool-use modifies the body schema. We hypothesized that, by modifying the somatosensory body schema, the use of a 40 cm-long mechanical grabber would affect the kinematics of subsequent grasping movements performed *without* the tool. Tool-use consisted of handling the grabber to reach and grasp a target object. Free-hand and tool-use grasping actions (see Supplemental Movies 1–4) were recorded in healthy subjects via a high-resolution optoelectronic three-dimensional motion tracking system by placing active infrared markers in the kinematically relevant locations on either the subject's hand or tool (Figure 1A).

In Experiment 1 ($N = 14$) separate ANOVAs with Sequence (pre/post tool-use) and target Size (small/large) as within-subject variables showed longer latencies (Velocity Latency (VL) $(1,13) = 11.62$, $p < 0.01$; Deceleration Latency (DL): $F(1, 13) = 15.11$, $p < 0.01$) and reduced maximal amplitude (peak) of reaching movement parameters after tool-use (Acceleration Peak (AP): $F(1,13) = 18.27$, $p < 0.01$; Velocity Peak (VP): $F(1,13) = 42.87$, $p < 0.01$; Deceleration Peak (DP): $F(1,13) = 21.50$, $p < 0.01$), as well as longer movement time (from action start to stable grip (MT): $F(1,13) = 15.05$, $p < 0.01$; all p-values Bonferroni corrected). Consistent with the tool property of allowing the subject to grasp objects with a 'longer' arm (see also Supplemental Figure S1), tool-use-dependent changes were selective for the transport component of the movement and independent of object size.

This pattern of results was confirmed by a replication study (Experiment 2, $N = 18$; Figure 1C), where five out of the six transport parameters shown to be affected in Experiment 1 were similarly modified. As in Experiment 1, no differences were present on the grasping phase of the movement. Critically, Experiment 3 ($N = 17$) ruled out unspecific test-retest effects possibly due to fatigue in handling the tool: when subjects performed the same tasks after training with a wrist-loaded weight (Figure 1B) identical to the tool weight (300 g), there was no change in any of the kinematic parameters (all p-values >0.4).

Our hypothesis that tool-use modifies the somatosensory representation of the subject's arm also predicts that different, previously untrained movements would be subsequently affected. We tested this prediction by assessing whether tool-use-dependent effects would affect a different type of free-hand movement, like pointing (see Supplemental Movies 5 and 6), which is composed of a transport phase, but was not trained with the tool (see Figure 1B). In Experiment 1, separate ANOVAs with Sequence and target Size as variables revealed that four out of the six transport parameters identified previously were similarly affected when free-hand pointing movements were performed after tool-use (AP: $F(1,13) = 8.07$, $p < 0.03$; VP: $F(1,13) = 16.22$, $p < 0.01$; DP: $F(1,13) = 14.15$, $p < 0.01$; MT: $F(1,13) = 24.11$, $p < 0.01$). In Experiment 2, all the six transport parameters were modified in the same direction, subjects showing longer latencies to achieve reduced peaks with longer movement duration (VL: $t(17) = -3.68$, $p < 0.01$; DL: $t(17) = -3.96$, $p < 0.01$; AP: $t(17) = 3.27$, $p < 0.01$; VP: $t(17) = 3.04$, $p < 0.01$; DP: $t(17) = -2.69$, $p < 0.03$; MT: $t(17) = -2.79$, $p < 0.02$; Bonferroni corrected p-values for both experiments). Again, no change was observed in the kinematics of pointing movements in control Experiment 3, in which the training consisted of grasping with the wrist-added weight.

The selective effects of tool-use on free-hand kinematics of grasping and their generalisation to pointing movements converge to strongly support the long-standing hypothesis that tool-use modifies the body schema. Because the object distance from the (hand and tool) starting position was fixed across experiments (Figure 1A) and within the hand reachable space, the kinematic changes can be selectively attributed to tool-use. At variance with most previous tool-use studies, in our experiments no widening of the reaching space was necessary during tool-use, ruling out any confound possibly due to perceptual differences of acting in different spaces. Moreover, we can exclude visual contributions in terms of 'shortening' of the perceived object distance [9], as acting on closer objects is known to affect kinematics in a different way, resulting in *shorter* latencies and reduced peak amplitudes.

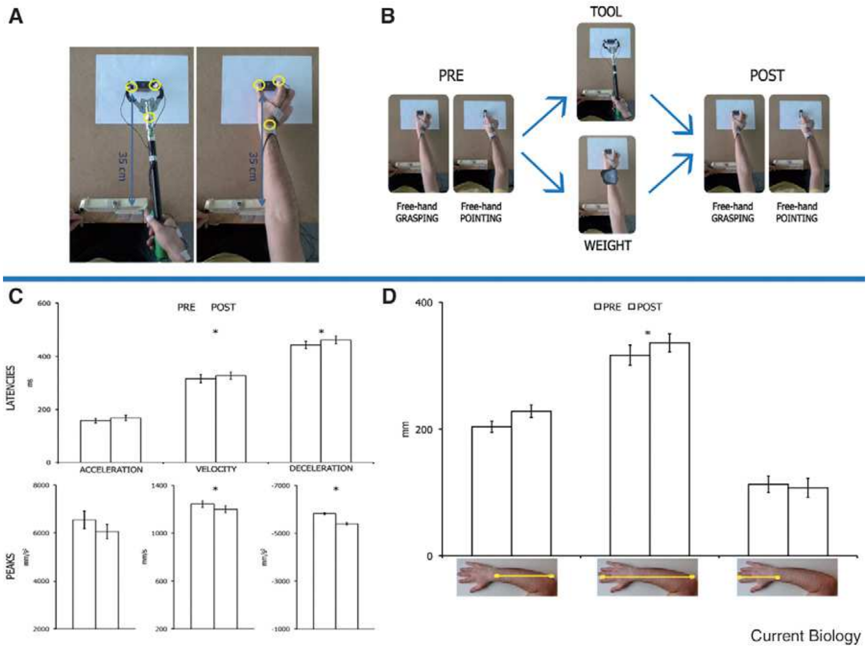

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Figure 1. Tool-use modifies movement kinematics and somatosensory morphology.

(A) Infrared emitting diodes (IREDs) were located on the hand and the tool (yellow circles) for three-dimensional motion recording and off-line kinematic analysis. Three functionally homologous positions were chosen on the tool (left panel) and the hand (right panel) according to their kinematic significance: thumb and index finger-tips provide grasping information while the wrist reflects hand transport. (B) Experiment time-course: pre training (left), grasping with the tool or the weight (centre), and post training (right). A differently oriented parallepiped located 35 cm from the starting position served as large (5 cm of graspable width) and small (2 cm) target for both free-hand (grasping and pointing) and training actions. (C) After the use of the tool, most parameters of the transport component of free-hand grasping movements were modified. Subjects show longer latencies (upper graphs) and reduced peak amplitudes (lower graphs). Movement time (not shown) was also longer after tool-use ($t(17) = -2.79$, $p < 0.02$, Bonferroni corrected). (D) Mean distance between the tactually stimulated anatomical landmarks (elbow-wrist, elbow-middle fingertip, wrist-middle fingertip) as localised by subject before and after tool-use. These results clearly show that after tool-use subjects rely on a modified somatosensory representation of their arm (i.e., a longer arm). Bar graphs illustrate mean values for each parameter ± s.e.m. Asterisks denote significant differences from one-tailed Bonferroni corrected paired-sample *t*-tests.

Our hypothesis specifies that the kinematic consequences of tool-use should reflect somatosensory changes in the body schema that are consistent with an increased length of the arm. We directly tested this further prediction in Experiment 4 (N = 12, see Supplemental Experimental Procedures) by asking blindfolded subjects to point with their left (untrained) index finger directly above the location of tactile stimuli that were randomly delivered to one of three anatomical landmarks (elbow, wrist, middle fingertip) of their right (trained) arm, before and after tool-use training. Figure 1D illustrates that the mean distance among the elbow and middle fingertip locations, as indicated by the subjects ending positions, increased after tool-use (Elbow-Finger $t(11) = -2.92$, $p = 0.03$, Bonferroni corrected). This task, originally introduced in neuropsychological cases to show body schema disruption or sparing (see Supplemental References), provides here direct evidence that what is modified by tool-use is the somatosensory representation of the arm morphology. In agreement with the transport selective effects of tool-use on kinematics, this change visually appears (Figure 1D) more related to the forearm than the hand.

The morphological updating of the body schema newly reported here does not require lengthy visuomotor adaptation, as no difference potentially due to learning the use of the grabber was observed during tool-use training (see Supplemental Figure S2). Although fast, the effects produced by tool-use were not ephemeral, and persisted (at least) for the duration of the post-tool sessions across three experiments (~10–15 min). Remarkably, grasping accuracy and the molar structure of free-hand movements [10] were not altered by tool-use. This suggests that the fast dynamic updating of body morphology induced by tool-use is functional, as it does not hamper the accurate and successful control of bodily movements.

Supplemental Data

Supplemental data are available at http://www.cell.com/current-biology/supplemental/S0960-9822(09)01109-9

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With this study we provided the first direct evidence of the plastic feature of the BS. After a relative short period of tool-use (around 15 minutes) subjects showed a modification of their kinematic profile while grasping a target object. The new kinematic profile was characterized by longer latencies of velocity and deceleration and reduced peaks amplitudes for acceleration, velocity and deceleration, as well as longer movement time (from action start to stable grip). No effect was found for the grip component, suggesting a selective update of the arm representation and not of the hand. The transport component is indeed affected by proximal arm joints while the grip component is a distal behaviour affected by fingers movement (Jeannerod, 1996).

As second main result, we found a generalization of the effects of tool-use to pointing movements, which were never performed with the tool. This excludes a possible interpretation of our main result as a practice-effect, in the sense of an acquisition of skilfulness due to the repetition of the same movement (grasping the object) over and over, since pointing movements were not trained. Moreover, against this explanation (effect due to skilfulness acquisition) is the fact that in that case we should have found a reduction of movement time after the use of the tool, and not an increase as we actually did. Rather, the generalization to the pointing movements strengthen the interpretation of the results as a consequence of a change in the arm length representation, since in this movement only the transport component is present.

We have been able to exclude the possibility that the new kinematic profile shown by the subjects after the use of the grab was due to a change in the perception of the object distance, and in particular to the object being represented as closer to the body. One could argue that giving the fact that the tool allowed to increase the extent of the reachable space, subjects could have just updated their spatial representation and processed the target object as being closer. Three arguments are against this explanation. The first comes from the set-up we used. During the entire experiment, the position of the object was always kept constant and the object was always placed inside the reachable space, precisely to avoid any possible confound due to acting in different regions of space. Second, previous studies have shown that reducing the distance between object and the grasping hand induces a shortening of latencies for the transport parameters and not an increase, as we actually observed after tool-use (Jeannerod, 1984; Gentilucci et al, 1991; 1992; Chieffi and Gentilucci, 1993). Third, the changes in kinematics observed when comparing pre-tool and post-tool movements are in the same direction as the natural difference shown by participants when compared on the basis of their arm length.

We also ruled out a possible causal role of muscle fatigue or movement repetition with experiment 3, where subjects performed the same number of grasping movements as in the tool-use phase, but with a tool-equivalent weight attached to the wrist. We found no effect of this type of training on the subsequent free-hand movements.

Finally, with experiment 4 we described the effect on the arm as a lengthening of its representation. The physical features of the tool we asked subjects to use in our study explain the selective update of the arm. It is indeed a long grab which main functional characteristic is to lengthen the arm by a distalization of the final effector, i.e. the fingers (Arbib et al. 2009). By the way, the length of the fingers of the tool as well as the maximal possible aperture was not different from an average human hand. This tool did not allow, for example, grasping objects larger than what the subjets' hand would have allowed. Overall, the results showed that the BS incorporates the action relevant features of the tool, by updating the body representation with its new metrical properties. This issue has been further addressed in the study 2, where we created a new type of tool that functionally modified the fingers length and thus enable a larger grip.

With this first study, we provided empirical evidence in favour of an old, intuitive idea that for almost a century has been present in the scientific literature as well as in the popular knowledge, i.e. that tools are incorporated in the body representation for action.

Moreover, we also validated the tool-use paradigm as a suitable one to induce BS plasticity and the pointing-to-touch as a powerful complementary task to access this plasticity. The second step has been to use our new powerful instruments to test the proposed dissociation between BS and BI in healthy subjects.

STUDY 2

When action is not enough: Tool-use reveals tactile-dependent access to Body Schema

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The aim of the second study was double. First, we wanted to test whether a modification of the BS, in healthy subjects, could be possible without any effect on the BI. In other words, we wanted to provide the (missing) dissociation between the body representation for action and perception in normal subjects.

In the first chapter of this thesis I described the main models of body representation. I also described how the development of the two-route model and its application to the somatosensory domain brought to the development of dyadic models composed by a body representation for action, the BS, and one for perception, the BI. Their existence and dissociation have been supported by many neuropsychological studies. Only recently, a dissociation has been shown between BS and BI in healthy subjects. In particular, Kammers and colleagues (2009; 2010) showed that the rubber hand illusion (RHI) affects the BI, leaving unaltered the BS. Using the tool-use paradigm that we proved being able to induce plastic changes in the BS, we tested for the opposite dissociation, namely its effect on the BS and not on the BI. To this aim, we designed motor and perceptual tasks to indirectly derive, from participants' behavior, the estimate of their (represented) arm length before and after a tool-use exercise. As predicted by the two-route model, the motor task should provide an access to the BS, while the perceptual ones are intended to test the BI. However, I already recalled the potential limits of this output-based approach. As suggested by Kammers and colleagues (2010), the risk here is to postulate the existence of as many representations as the number of tasks we can design. Therefore, as a second aim of the study we investigated the role of the input in accessing the different body representations. In a 2x2 design, we coupled motor and perceptual tasks with two entry modalities for defining the target body sites of each task, which were either tactually or verbally identified. In four separate experiments, we asked subjects to either point or perceptually localize the position in space of three tactually stimulated or named anatomical landmarks on the right arm, before and after tool-use performed with the right arm. Distances among the localized three targets were calculated off-line and compared to test for an effect of the use of the tool on the representation of the subjects' arm length. According to the two-route model and the results of our previous study, we predicted that only the motor task would show the modification in the arm length estimation and not the perceptual one.

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When action is not enough: Tool-use reveals tactile-dependent access to Body Schema

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ABSTRACT

Proper motor control of our own body implies a reliable representation of body parts. This information is supposed to be stored in the Body Schema (BS), a body representation that appears separate from a more perceptual body representation, the Body Image (BI). The dissociation between BS for action and BI for perception, originally based on neuropsychological evidence, has recently become the focus of behavioural studies in physiological conditions. By inducing the rubber hand illusion in healthy participants, Kammers et al. (2009) showed perceptual changes attributable to the BI to which the BS, as indexed via motor tasks, was immune. To more definitively support the existence of dissociable body representations in physiological conditions, here we tested for the opposite dissociation, namely, whether a tool-use paradigm would induce a functional update of the BS (via a motor localization task) without affecting the BI (via a perceptual localization task). Healthy subjects were required to localize three anatomical landmarks on their right arm, before and after using the same arm to control a tool. In addition to this classical task-dependency approach, we assessed whether preferential access to the BS could also depend upon the way positional information about forearm targets is provided, to subsequently execute the same task. To this aim, participants performed either verbally or tactually driven versions of the motor and perceptual localization tasks. Results showed that both the motor and perceptual tasks were sensitive to the update of the forearm representation, but only when the localization task (perceptual or motor) was driven by a tactile input. This pattern reveals that the motor output is not sufficient per se, but has to be coupled with tactually mediated information to guarantee access to the BS. These findings shade a new light on the action–perception models of body representations and underlie how functional plasticity may be a useful tool to clarify their operational definition.

1. Introduction

A peculiar relationship exists between the body and the brain, the latter being physically inside the former, but at the same time being the master. The brain receives information from and sends commands to the entire body. This dialectic relationship suggests that body and brain shape each other in a continuous exchange of information (Gallagher, 2005) with the essential goals of successfully interacting with the environment and preserving life. To succeed in these tasks, the brain needs to represent the body in a way that is useful for the specific activity it performs at a given time, which implies, for example, to represent the body differentially for perception and action (Cardinali, Brozzoli, & Farné, 2009; Dijkerman & De Haan, 2007). This functional feature underpins dyadic as well as triadic models of body representation proposed in the literature since the seminal neuropsychological work by Head and Holmes (1911–1912). They suggested the existence of (at least) two representations: The Postural Schemata (later termed Body Schema, BS), hypothesized to serve the guidance of actions and being mainly constructed on proprioceptive and tactile information, and the Superficial Schemata (later termed Body Image, BI), which would instead serve perception and be formed mainly by visual, but also other sensory inputs.

Neuropsychological work from Paillard, Michel, and Stelmach (1983) established the action–perception distinction in the somatosensory domain by reporting a patient who, after a left

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parietal lesion, was unable to detect touches on the contralesional deafferented hand, but could accurately point to them in 40% of the trials, thus revealing a blind-sight phenomenon in the tactile modality (see also Rossetti, Rode, & Boisson, 1995). Anema et al. (2009) recently extended this dissociation at higher levels of somatosensory processing, when tactile detection abilities are spared by the brain lesion. They asked two stroke patients to localize a tactile stimulus by either pointing directly to their tactually stimulated hand (hand task), or to a visual map of the hand (map task). The first task involved the body representation for action (i.e., the BS), as it relies mainly on unconscious "online processing and integration of proprioceptive and tactile input" (p. 1620), whereas in the second task the felt touch had to be consciously integrated with a stored representation of the hand's visual features (i.e., the BI). The authors reported a double dissociation, as one patient was impaired in the map task, but not in the hand task while the other patient displayed the opposite pattern. Overall, these findings strengthen the functional principle of division of labour between body representations, akin to the perception–action distinction proposed for vision and touch (Dijkerman & De Haan, 2007; Milner & Goodale, 1995) and support the existence of multiple representations of the body (see, for review, de Vignemont, 2010; Schwoebel & Coslett, 2005; Sirigu, Grafman, Bressler, & Sunderland, 1991). In particular, relative consensus exists on the definition of BS, which has been closely associated to its unconscious, action-devoted nature, whereas vagueness still persists in the description of the BI, frequently associated with the conscious, perceptual scrutiny of body features (de Vignemont, 2010).

A crucial feature of body representations is their plasticity, which arises from the need for the brain to update body representations according to both the slow and fast changes the body undergoes with time. Owing to the notion that different body representations are built and accessed to for different purposes, it has been proposed that they can also be updated selectively (deVignemont & Farnè, 2010). Kammers, de Vignemont, Verhagen, and Dijkerman (2009) provided evidence for a selective modification of the BI, to which the BS was immune, in physiological conditions. They proceeded by first inducing in healthy subjects the phenomenon of the Rubber Hand Illusion (RHI), in which synchronous visual-tactile stroking of the participant's real hand (unseen) and a plausibly oriented (visible) rubber hand evokes the feeling of ownership of the rubber hand and, of particular interest here, also induces a proprioceptive bias such that participants localize their hand as being closer to the rubber hand (Botvinick & Cohen, 1998; Ehrsson, Holmes, & Passingham, 2005; Folegatti, de Vignemont, Pavani, Rossetti, & Farnè, 2009; Tsakiris & Haggard, 2005). Kammers and colleagues then assessed the proprioceptive bias by requiring either perceptual tasks (i.e., recruiting the BI), or motor tasks (i.e., recruiting the BS). A perceptual task consisted in a visually based task in which subjects watched the experimenter's right and left fingers moving along a line perpendicular to their sagittal axis. In order to judge the proprioceptively perceived position of their index fingers, they had to (verbally) stop the experimenter when they thought the moving fingers were just in front of each of them. Another perceptual task consisted of choosing, among differently sized wooden sticks, the one whose length matched the perceived distance between their right and left index fingers. One of the two motor tasks consisted in a ballistic pointing, performed using either the right (stimulated) or the left (unstimulated) hand to localize, respectively the (unseen) left or right hand. In the other motor task, participants were required to use both index fingertips to reach the extremities of a stick horizontally arranged in front of them. The authors reported that, after induction of the RHI, healthy subjects were biased in localizing their own hand when the task was perceptually based, but not when it was action-based, thus providing a simple dissociation supporting the hypothesis that body representations can be selectively updated (Kammers et al., 2009; Kammers, Kootker, Hogendoorn, & Dijkerman, 2010).

The present study aimed at further assessing the selectivity of the plastic updating of body representations. As a first aim, we tested the case for the opposite dissociation to that reported by Kammers and colleagues. To this aim, we took advantage of a novel sensorimotor paradigm we recently introduced for assessing the changes in metrical aspect of the forearm representation after the use of a tool (Cardinali, Frassinetti et al., 2009). By comparing the kinematics of free-hand movements performed before and after the use of a mechanical grabber that increased subjects' arm-length, we showed that movement execution was modified after tool-use. Both grasping and pointing movements were characterized by different kinematic profiles after grasping objects with a 40 cm-long tool. Noteworthy, this difference was compatible with an increase of the represented length of the arm. The temporary increase of the internally represented arm-length, compatible with the idea that tool-use can update the BS, was supported by the fact that, when asked to point to the tactile stimuli that were delivered to their tool-trained forearm, participants pointed to locations that were farther apart. Building onto well-established task-dependent access to either the BS or the BI, here we used motor and perceptual tasks to assess whether the metric of body representations can be updated selectively, namely whether tool-use may affect the BS without altering the BI. Pointing to tactile stimuli delivered on anatomical landmarks of the forearm operating the tool, as in Cardinali, Frassinetti et al.'s work (2009), was used to assess for changes in the BS, whereas visual localization of the same anatomical landmarks was used to probe changes in the BI.

As a second aim, we assessed whether the way subjects are informed about the to-be-localized targets may play a discriminating role in determining which body representation is used. To date, the hallmark of the dissociation between body representations is the outcome: different results emerge when participants perform different tasks (perceptual vs. motor) on the very same incoming information. Neuropsychological work by Rossetti et al. (1995), however, already pointed out that the same tactile localization task may bring to opposite findings as a function of whether motor (BS) or verbal (BI) modalities are used by the patient. Here we hypothesized that using somatosensory or verbal indication as different entries for the same task of pointing to, or visually localizing the anatomical landmarks on the participants' forearm, may bring to a different pattern of results. As suggested by Kammers, Mulder, de Vignemont, and Dijkerman (2010), a better understanding of the level of dissociation among body representations should pass through a more complete approach which uses not only an output-type of criterion, but also considers the input used to trigger the same task.

To jointly address these aims, we ran a series of four experiments in which we asked healthy participants to localize three landmarks on their forearm either through a motor task (Experiments 1 and 2), or a perceptual task (Experiments 3 and 4), to indirectly estimate the represented length of their arm, before and after the use of a tool. Crucially, the two types of tasks could be triggered by the experimenter either touching (Experiments 1 and 3), or naming (Experiments 2 and 4) each target body-part. As the BS is motor in nature, and essentially fed by somatosensory inputs, we predicted to observe a modification of arm-length representation after tool-use in the motor, but not in the perceptual task, and when subjects were asked to localize touched, but not named, body-parts. If the BI is immune to the tool-use-dependent plasticity, the perceptual task should be unaffected, particularly when subjects were asked to localize named body-parts

2. Motor tasks (Experiments 1 and 2)

2.1. Participants

Thirty (12 males; mean age 25 years; range 18–34) subjects participated in the study and were randomly assigned to one of the two experiments (fifteen participants each). All except one were right-handed according to the Edinburgh Handedness Inventory and had normal or corrected to normal vision and no history of neurological or psychiatric disorders. All participants gave verbal informed consent to participate to the study which was approved by the board of the INSERM ethics committee.

2.2. Methods

Before the experimental session, typical anthropometric parameters were manually derived to measure the subject's forearm and hand length, by using the same anatomical landmarks used as targets in the experiments (see below). Both experiment were composed of three phases: A pre- and post-tool-use session (18 trials each) during which the action-based task was executed (see below), separated by a tool-use session. The latter consisted of 4 blocks of reach-to-grasp movements (12 trials each) that were executed with a hand-held 40 cm long mechanical grabber. Subjects were instructed to lift and replace the grasped object in its original position, before going back to the starting point. The grabber, composed by an ergonomic handle with a lever, a shaft and two "fingers" was used to reach, grasp, lift and replace a plastic parallelepiped that served as a target object.

Subjects were blindfolded and comfortably seated in front of a table. The experimenter positioned their right forearm on a horizontal wooden support with an inclination of 45° with respect to subject's body mid-line. The anatomical target sites were shown to subjects and then a wooden pointing-board was placed over the arm, at a distance of 4 cm from the skin surface. Three IRED markers (infrared emitting diodes) were placed on the subject's right arm, respectively on the tip of the middle finger, the wrist and the elbow. A forth marker was placed on the left index fingertip that participants used to point to the touched target body-part (see below). A high-resolution motion tracking system (Optotrak 3020, Northern Digital Inc., Ontario, Canada) was used to record markers' position over time (200 Hz). In both experiments, participants were asked to point quickly and precisely with their left forefinger to one of three anatomical sites of the right arm (middle fingertip, wrist, elbow). Subjects were randomly assigned to the 'tactile' (Exp. 1) or 'verbal' (Exp. 2) experiment, differing as to the way the anatomical target site was designated upon each trial: the experimenter either touched the target body-part, via a manually operated electronic von Frey aesthesiometer (ITC Inc., California), or verbally named the target. An acoustical signal informed the subject of the beginning of a trial. The distance between the mean landing positions of the left index fingertip was used to indirectly derive an estimate of subjects' representation of their arms' length, before and after tool-use. To this purpose, two measures were computed: the distance between elbow and wrist (i.e., Forearm-e) and wrist and fingertip (i.e., Hand-e). As such, subjects were never instructed to make an explicit length judgment. The distance among the IRED markers position on the same anatomical landmarks served to compute the real physical length of the subjects' right arm (Hand-r and Forearm-r). All distances were calculated on x–y coordinates (i.e., on a 2D plane).

2.3. Results

First, we analysed for each experiment the indirectly derived estimate of the represented length of the hand (Hand-e) and forearm (Forearm-e) obtained before tool-use and compared (paired t-test, two-tail) with the participants' real hand (Hand-r) and forearm (Forearm-r) lengths, as derived from the IREDs position. To assess whether tool-use-induced plasticity affected the subjects' represented morphology the pre-tool-use average values for each estimated length were compared (paired t-test, one-tail, Bonferroni corrected) to post-tool-use values (i.e., without deducting the real distance).

In Experiment 1 (tactile-to-motor) comparing the estimated length of each segment revealed that the Hand-e (141 mm) was shorter than the Forearm-e (226 mm; $p < .02$). This pattern reflects the actual morphology of the subjects. When comparing actual with estimated lengths, by expressing the latter as the proportion of the former, participants pointed to the anatomical landmarks as if their hand was underestimated (Hand-e = 80% of Hand-r; $p = .02$). A similar, albeit non-significant trend was observed for the forearm length (Forearm-e = 93% of Forearm-r; $p = .40$).

After tool use, a significant increase in the Forearm-e distance was found. Fig. 1B illustrates that subjects pointed according to an elongated arm representation when stimulated on the wrist and the elbow (mean length 226 vs. 241 mm; $p = .04$). No difference was observed after tool-use for the Hand-e (141 vs. 140 mm; $p = .90$). To check for consistency of such an effect, participants' performance was inspected on a single-subject basis. To this purpose, the pre–post difference in the distance among mean landing positions was calculated for each subject (post-tool-use distance minus pre-tool-use distance = tool-use effect) to determine the proportion of subjects similarly affected by tool-use. Fig. 2A illustrates both increase (positive values) and decrease (negative values) in the represented morphology of the Forearm-e length after tool-use. The large majority of the subjects (12 out of 15 = 80%) displayed an increase in the estimated arm length after tool-use.

Similarly to Experiment 1, in Experiment 2 (verbal-to-motor) before tool-use subjects were accurate in their pointing performances, as the proportion among the hand and forearm segments was reflected in the hand being estimated as shorter than the forearm (Hand-e = 114 vs. Forearm-e = 224 mm, $p < .02$). Again, the underestimation of the hand as compared to its actual size (Hand-r = 173 mm) was significant, the Hand-e representing the 67% of the actual length of the hand ($p < .02$). The underestimation was not significant for the forearm (Forearm-e = 94% of Forearm-r; $p = .66$).

When the same pre–post tool-use comparisons as in Experiment 1 were considered (see Fig. 1B), no differences were found for the two segments between pre- and post-tool-use training sessions (Forearm-e = 224 vs. 229 mm; $p = .40$; Hand-e = 114 vs. 110 mm; $p = .54$). The absence of significant tool-use dependent effects was reflected in the small proportion of subjects showing consistent changes in the estimated wrist-elbow distance. Fig. 2B illustrates that roughly half of the participants (8 out of 15 = 53%) displayed an increase in the estimated arm length after tool-use.

2.4. Discussion

When pointing to touched, but not named body-parts after the use of the grabber, subjects localized their forearm extremities as if they were farther apart. As such, the indirect estimation of their forearm length appeared to be increased in the tactually driven experiment. This result is in line with a previous study (Cardinali, Frassinetti et al., 2009), where we showed a modification of the fingertip-elbow (i.e., the Total-e) distance after tool-use. Noteworthy, here we found that the significant increase was selective for the Forearm distance, in keeping with Cardinali and colleagues' kinematics findings, showing that using a tool that functionally extends the arm by 40 cm affects the kinematics of the reaching (arm related), but not the grasping (hand related) phase of

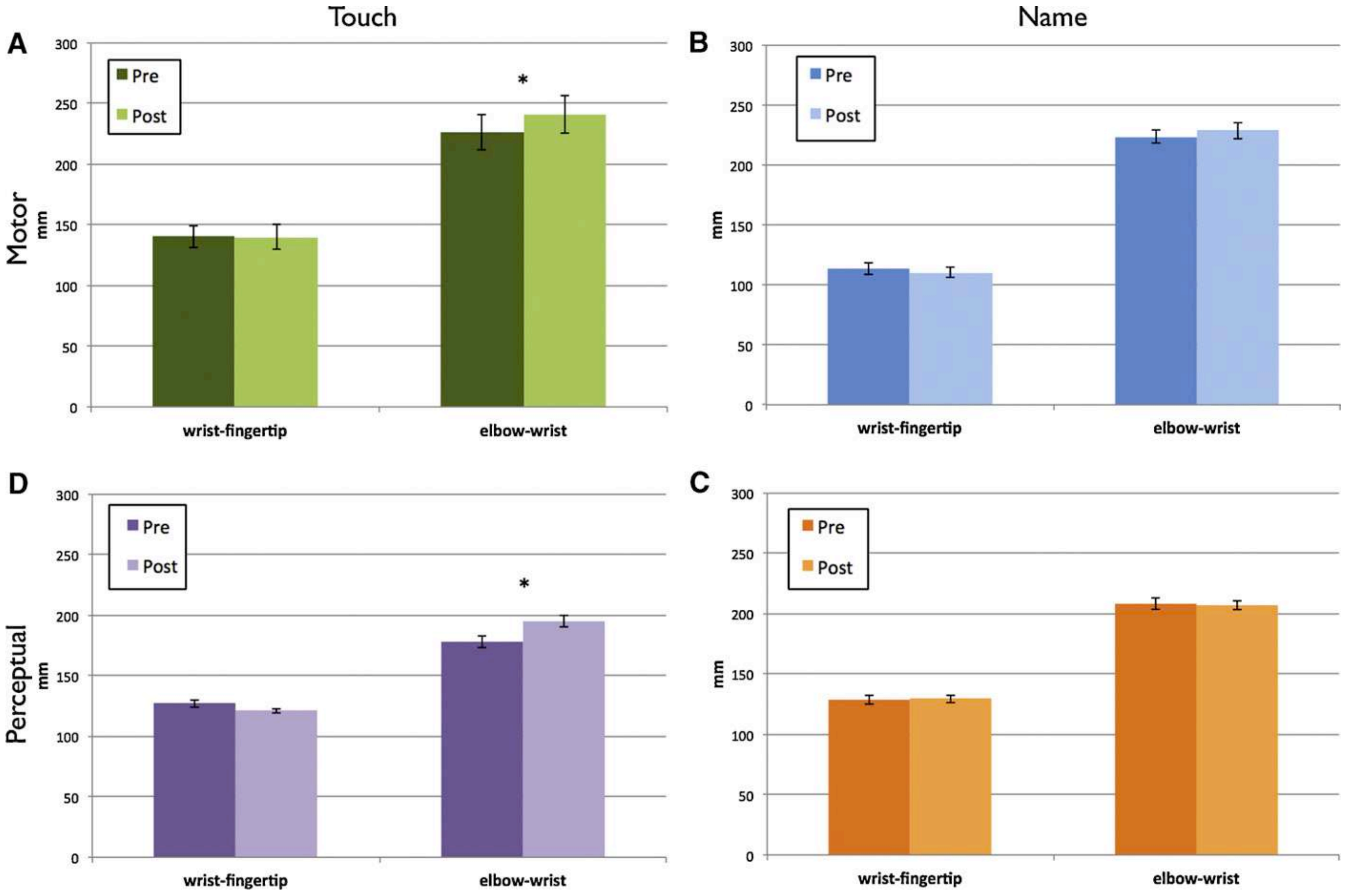

Fig. 1. Mean length estimation for the forearm and hand segments before and after tool-use for the four experiments. Error bars represent the standard error mean (SEM).

prehension movements. In that study, we additionally showed that performing as many grasping movements as in the tool training of this study, with a tool-equivalent weight attached to the wrist, did not affect the subsequent kinematics of free-hand movements (Cardinali, Brozzoli et al., 2009; Cardinali, Frassinetti et al., 2009: Experiment 3). Therefore, we attribute the increase in arm length representation reported here to tool-use, rather than general sensorimotor effects.

According to action/perception models of body representations, we used a motor task to be able to access the body representation for action, i.e., the BS. Importantly, since the BS has been described as a mainly somatosensory-based representation (de Vignemont, 2010; Head & Holmes, 1911–1912), in Experiment 1 this motor output was coupled with a tactile input. With this particular configuration of input–output modalities, it has been possible to reveal a tool-use-induced plasticity of the BS that, in sharp contrast, was absent in Experiment 2. When pointing movements were triggered by a verbal label of the anatomical target, no significant difference in length estimation was observed in none of the measured segments, despite the very same motor output was required. These results reveal that the motor output is not a sufficient condition for accessing the BS. They further imply that a strictly output-based experimental approach is not complete and could fail in revealing plastic features of body representations. Moreover, they clearly suggest a key role in assessing the BS is played by the tactile input. These points will be addressed thoroughly in the general discussion.

3. Perceptual tasks (Experiments 3 and 4)

3.1. Participants

Thirty (14 males; mean age 24 years; range 19–34) subjects participated in the experiments. All but four were right-handed according to the Edinburgh Handedness Inventory and had normal or corrected to normal vision and no history of neurological or psychiatric disorders. All participants gave verbal informed consent to participate to the study, which was approved by the board of the INSERM ethics committee.

3.2. Methods

As in the previous experiments, there were three phases: a pre- and post-tool-use session (18 trials each) during which the perceptual-based task was executed (see below), separated by a tool-use session. This session was identical to the one in Experiments 1 and 2. Procedures were identical to Experiments 1 and 2 except what specified below. Subjects were seated in front of a table and their right arm laid on a 20 cm-high support (Experiment 3) or directly on the table (Experiment 4) so that the mid-point was aligned with subjects' mid-line. In both experiments, the arm was hidden by a suspended black fabric that prevented its vision. In Experiment 3, the arm support allowed the experimenter to precisely deliver unseen touches at the three arm locations. The distance between the arm and the meter was identical between experiments: 40 cm away from and parallel to the arm. At the

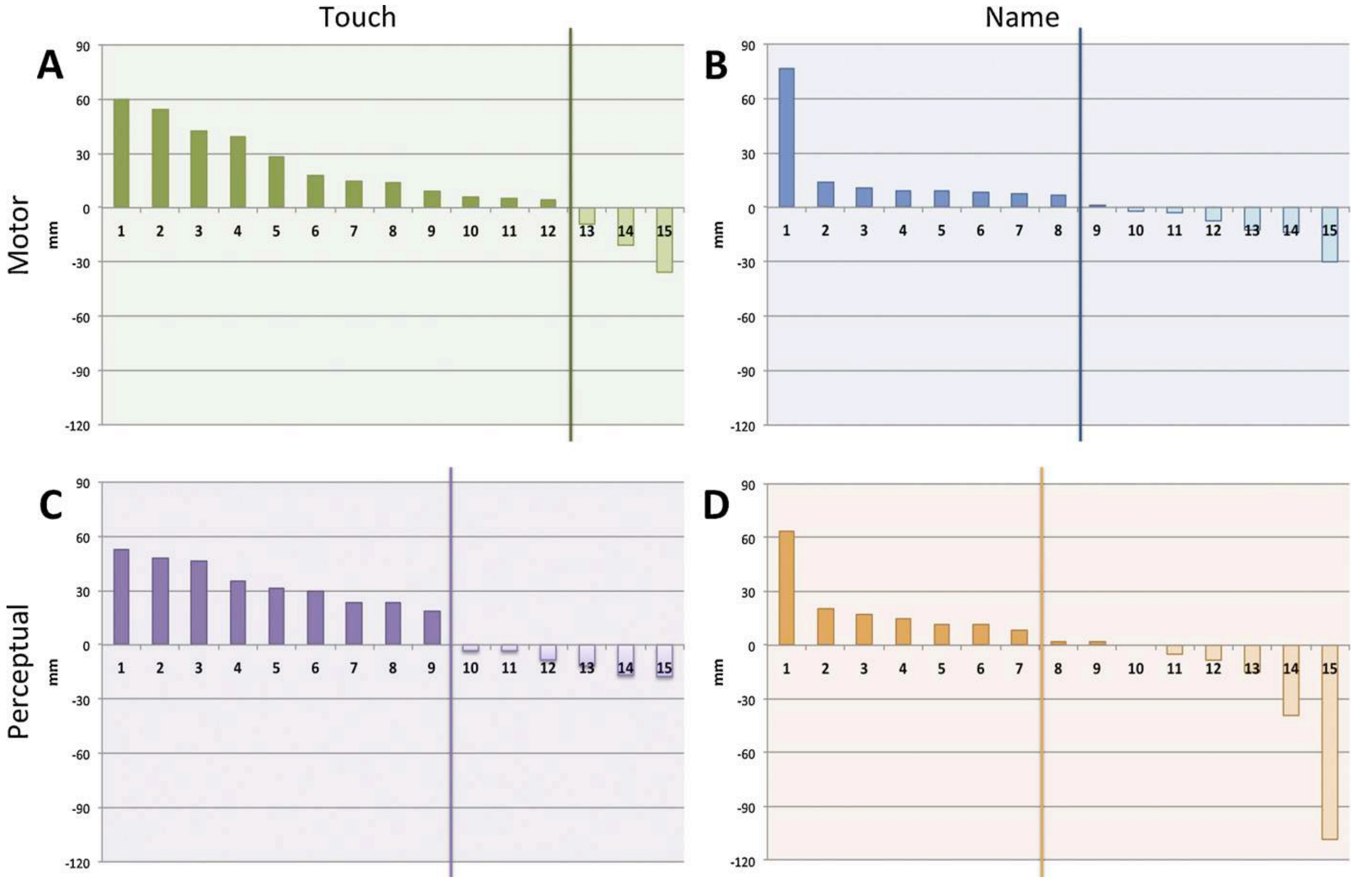

Fig. 2. Difference between post- and pre-tool use in the represented forearm length for each subject in the four experiments. Positive values indicate an increase in the indirectly estimated length after tool-use, negative values a decrease.

beginning of each trial subjects were asked to close their eyes while the experimenter was changing the lateral offset of the meter. This was done to avoid any possible calculations from previous trials. Then the subjects were asked to open their eyes and the experimenter either touched (Exp. 3) or named (Exp. 4) one of the three anatomical targets (middle fingertip, wrist or elbow) just as in Experiments 1 and 2, respectively. In both experiments, subjects had to verbally report the number on the meter corresponding to the perceived position of the (unseen) anatomical target. After each trial, subjects were instructed to close their eyes and wait for the experimenter's instruction to open them again.

3.3. Results

Similarly to the previous experiments, in both Experiments 3 and 4 subjects' indirect estimates of their forearm and hand representation, as measured before tool-use, respected their real morphology (Exp. 3: Forearm-e = 178 mm vs. Hand-e = 126; $p < .02$; Exp. 4: Forearm-e = 208 mm vs. Hand-e = 129; $p < .02$). Also similarly to Experiments 1 and 2, when compared with the real sizes, the hand was significantly underestimated (Exp. 3: Hand-e = 64% of Hand-r; $p < .02$; Exp. 4: Hand-e = 65% of Hand-r; $p < .02$). Additionally, we found a significant underestimation for the forearm too (Exp. 3: Forearm-e = 73% of Forearm-r; $p < .02$; Exp.4: Forearm-e = 82% of Forearm-r; $p < .02$).

When comparing pre- with post-tool-use localization performance in Experiment 3 (tactile-to-perceptual) a significant increase in the Forearm-e distance was found. Fig. 1C illustrates that subjects pointed according to an elongated arm representation when stimulated on the wrist and the elbow (mean length 178 vs. 194 mm; $p = .04$). No difference was observed after tool-use for the Hand-e (126 vs. 121 mm; $p = .74$). Fig. 2C represents single subjects' performance for the Forearm-e segment. The majority of the subjects (9 out of 15 = 60%) displayed a consistent increase in the estimated arm length after tool-use.

On the contrary, and similarly to Experiment 2, when subjects' localization performances were compared to assess for the effect of tool-use in Experiment 4 (verbal-to-perceptual), no differences were found between pre- and post-tool-use sessions among the two distances (Hand-e = 128 vs. 129; $p = .86$; Forearm-e = 208 vs. 207; $p = .86$; Fig. 1D). Again, inspection of single subject's performance makes clear that no consistent effect was present, about half of the subjects (7 out of 15 participants = 47%) showing an increase and the other half a decrease in estimated lengths (see Fig. 2D).

4. Discussion

When making perceptual localization judgements of touched, but not named body-parts after the use of the grabber, subjects localized their forearm extremities as if they were farther apart. Similarly to the pattern of results observed in Experiments 1 and 2, the indirect estimation of the participants' forearm length appeared to be increased only in the tactually driven experiment. According to action/perception models of body representations, we used a perceptual task to be able to access the body representation for perception, i.e., the BI. Owing to the fact that our tool-use approach emphasises action rather than perception, we predicted that the BI would not be affected. In this context, since conscious access to the metric of the BI via verbal tasks has been proven to be sensitive to functional updating following the induction of the rubber hand illusion (Kammers et al., 2009), and to be detrimental to the access of the BS (Rossetti et al., 1995), in Experiment 4 we coupled the perceptual output with a verbal input. This particular configuration of input–output modalities, which would thus represent the best expression of BI's features, failed to show any tool-use-dependent effect that would have been genuinely attributable to the BI. In this respect, the results are in keeping with what one should have expected based on the available literature (de Vignemont, 2010; Kammers et al., 2009). However, using a perceptual type of output did not appear to be sufficient to make the BI fully immune to tool-use-dependent plasticity. Despite the very same perceptual output was required, when perceptual localization judgements were triggered by a tactile input a significant increase in length estimation was observed. Remarkably, this increase was selective for the forearm, similarly to the increase observed in Experiment 1, whereby a motor output was required. These results suggest that whether the BI is affected or not by motor manipulations (here tool-use) may quite substantially depend on which features of this body representation are emphasised in the combination of the input modality and output task. Furthermore, these findings clearly demonstrate that a strictly output-based experimental approach to the study of body representations is limited. Moreover, they open the question as to whether and to what extent body representations operate separately in physiological conditions, in that the tool-use dependent effect found in experiment 3 under tactile input conditions may have affected the BI ether directly, or indirectly via the (almost identical) change in BS already shown in Experiment 1. These points will be further discussed below.

5. General discussion

In this study we addressed the issue of the independent existence and functioning of two body representations, the Body Schema and the Body Image, in physiological conditions. Among the four experiments we conducted, two of them were designed to maximize the involvement of one of the two representations, reducing at the minimum the possible contribution of the other. In particular, in Experiment 1 we coupled a motor task with a tactile entry: this task was conceived to selectively access the BS, which is a body representation devoted to action whose update is based on somatosensory information (de Vignemont, 2010; Head & Holmes, 1911–1912). As predicted, and in agreement with our previous work (Cardinali, Frassinetti et al., 2009), results showed an increase in the represented forearm length that was compatible with an incorporation of the tool. In contrast, in Experiment 4 we used a perceptual task triggered by a verbal input, which was assumed to selectively tap into the BI. With this input–output combination, we could not find any modification in the represented arm length, suggesting that the perceptual representation of the body (BI) cannot incorporate tools. This first comparison suggests that the incorporation of tools takes place in the BS, leaving the BI unaffected. Considered together with the results of Kammers et al. (2009), Kammers, Kootker et al. (2010) on the effect of the RHI on the BI, but not on the BS, these data provide the missing dissociation in healthy individuals necessary to support the existence of two separated body representations for action and perception.

The question of how many body representations exist in the human brain has a long history (Bonnier, 1905), mainly inferred from the differential performance of neurological patients. When in 1911 Head and Holmes observed a patient (HR) who was not able to appreciate passive changes in body-parts posture, but could perfectly report tactile stimulations on the same body-part, they proposed that these two bodily related abilities (posture appreciation and touch localization on the skin surface) were based on the existence of at least two separated representation (respectively the BS and the BI). The double dissociation approach has been commonly applied to describe BS and BI in neuropsychological studies (Anema et al., 2009; Cole & Paillard, 1995; Paillard et al., 1983), leading to dyadic or triadic models of body representations that, besides their differences, agree in conceptualizing the existence of a motor representation (BS) and a perceptual one (BI). However, despite several models have since been proposed (Buxbaum & Coslett, 2001; Cole & Paillard, 1995; Gallagher & Cole, 1995; Schwoebel & Coslett, 2005; Sirigu et al., 1991), the type and the functional features of these representations remain highly debated (de Vignemont, 2010).

These models have been largely influenced by the two-routes model for perception and action (Dijkerman & De Haan, 2007; Milner & Goodale, 1995), according to which the goal of the subject determines the type of representation and the neural structures that will be used to accomplish the task. Applied to the body representation domain, this model proposes that depending on the nature of the task (motor or perceptual) one of the two representations will be used (the BS or the BI). The output modality has thus become the main criterion to disentangle between BS and BI. In particular, the BS has been tested through motor tasks like ballistic pointing, whereas perceptual tasks like verbal reports have been used to access the BI.

However, it has recently been pointed out that this essentially output-based approach can be reductive and potentially misleading. First, the mere presence of a motor act is not a sufficient criterion to presume an involvement of a motor-related processing. Milner and Goodale (2008) already suggested in the visual domain that the fact that the subject is asked to give a motor response does not mean that the sensory information will be processed in the dorsal stream if the task is not motor in nature. Króliczak, Heard, Goodale, and Gregory (2006) recently showed that the same motor action (pointing) can rely on different stream processing depending on the way it is performed: Ballistic pointing relies on information processed in the dorsal stream and is immune to a perceptual illusion, whereas a slow pointing implies the activation of the ventral stream and is highly influenced by perceptual distortions. In addition, depending on the mode of pointing (communicative vs. motor), different performance can be observed (Cleret de Langavant, Trinkler, Cesaro, & Bachoud-Lévi, 2009). Second, as noted by Kammers, Kootker et al. (2010), focusing on task dependent dissociations may misleadingly overestimate the number of 'necessary' body representations if taken in isolation without considering the input, as well as the input–output interplay (Kammers, Kootker et al., 2010). Such an implication is clearly demonstrated by studies of the same group. When comparing perceptual with motor responses in a typical RHI setting, Kammers and colleagues found that inducing the RHI had selective effects on the BI, as derived by changes in perceptual measures of proprioception, but did not alter the BS, whose motor measures did not change (Kammers et al., 2009). When, however, similar output comparisons were made after modifying the input (e.g., by stroking both index and thumb of a 'grasping' rubber hand), motor responses became more illusion-sensitive (Kammers, Mulder et al., 2010). Importantly, Newport, Pearce, and Preston (2010) recently reported that both representations can be affected, as shown by perceptual and pointing tasks, if the RHI is induced through the real-time observation of active movements of one's own hand over a paintbrush, that is, when the weight of proprioceptive and tactile information is stronger than in the classic RHI. Finally, besides the differences owing to the temporal dynamics and weights attributed to different sensory modalities, the BS and BI also differ in terms of the level of consciousness (Gallagher, 2005; Kammers, Mulder et al., 2010).

Here we tested whether the BS can be selectively updated following a sensorimotor manipulation by trying to overcome the limits of the output-based approach and manipulating not only the output, but also the input modality. Motor and perceptual outputs designed after previous studies (Cardinali, Frassinetti et al., 2009; Kammers et al., 2009; Tsakiris & Haggard, 2005) were combined with tactile and verbal inputs. Tactile and verbal entries were chosen, as they are most likely to put at stake the BS and the BI, respectively. Tactile information is indeed of great relevance in performing actions. Already Head and Holmes evidenced the BS is updated through sensory information evoked by posture alteration, which suggests a key role of proprioception in the updating process. Moreover, it has been shown that mechanoreceptors from the skin can provide important information about hand posture and thus contribute to postural control during grasping (Edin, 1992). Finally, the use of the tactile cue to trigger a pointing movement does not necessarily demand a conscious processing of the body-part metrics, which means that the BS, whose update is unconscious, can use this type of information. On the other hand, verbal information implies a more conscious elaboration to lead to the identification of a specific body-part that has to be localized. Neuropsychological studies by Rossetti and colleagues (Rossetti et al., 1995; Rossetti, Rode, & Boisson, 2001) showed that using verbal processing at the output level accessed a different body-part metrics, and was powerful enough to disrupt the residual intact capabilities of the BS.

By strengthening the output modality with the appropriate sensory input, the present study showed a dissociation between the two body representations. However, because of the particular design we used,[1] with the Experiments 2 and 3 we have also been able to go beyond the dissociation and test for a possible interaction between BS and BI. Indeed, while in Experiments 1 and 4 the input–output combination was totally unbalanced towards one body representation, Experiments 2 and 3 represent the intermediate positions between two extremes, allowing for the typical input of the BS (touch) to be assessed with the typical output feature of the BI (perceptual), and vice versa. Considering, for example, only the output of the Experiment 2 (a pointing movement), one would expect to find a result similar to the tactile triggered pointing Experiment 1. Critically, however, Experiment 2 showed that the increase in the participants' represented arm length depends on the type of input: After tool-use, pointing to the same, but verbally identified target landmark on the forearm was ineffective. Noteworthy, such a differential pattern emerged despite the very same motor pointing task was used and the same visual information about landmarks position was allowed before starting the open-loop pointing in each experiment. By manipulating the opposite side of the input–output chain, we show here for the first time that whether the entry information is provided tactually or verbally, it may determine whether the BS is accessed or not, proving that the motor output is not a sufficient element for accessing the BS.

Interestingly, when testing for the opposite tactile input – perceptual output combination in Experiment 3, we found a significant effect of tool-use on the represented forearm length, also in the direction of tool-incorporation. Again, this result would not have been predicted by a merely output-based rationale: Considering only the output of the Experiment 3 (a perceptual judgment), one would expect to find a result similar to the verbally triggered judgment of Experiment 4. In sharp contrast, not only an effect of tool-use was found, but this was remarkably similar to that observed in Experiment 1: the increase in the represented arm length was selectively dependent upon the forearm, without affecting the hand (see Fig. 1). This finding is compatible with two, non-mutually exclusive interpretations: tool-use might have affected the BI either directly or indirectly, via the effect that tool-use is known to exert on the BS (Cardinali, Frassinetti et al., 2009 and Experiment 1). While it is difficult on the basis of the present work, and outside its scope, to definitively disambiguate these possibilities, we believe that the high selectivity of the tool-use effect on the forearm lengthening speaks in favour of an indirect, BS-mediated influence over the BI. This would indicate that the tactile input is sufficient to provide an access to the BS.

Our study provides an additional main finding: in relatively static conditions the metric representation of the forearm is not substantially different when investigated through motor/tactile (BS) or perceptual/verbal tasks (BI). In all the four experiments, the existing proportion among the arm segments was maintained as subjects estimated their hand as being shorter than the forearm, although the estimated sizes did not perfectly reflect the real ones. Overall, the hand representation appeared to be shortened, as already reported previously (Cardinali, Brozzoli et al., 2009; Cardinali, Frassinetti et al., 2009; Longo & Haggard, 2010), the same shortening being present for the forearm. We thus suggest that an additional theoretically relevant aspect to be manipulated when comparing performances aimed at distinguishing between body representations is to tackle their sensitivity to plastic changes, rather than solely relying on the access to relatively static features of these representations. This is clearly exemplified by the present study, when comparing the findings on morphological representation of the forearm obtained before any plastic manipulation had being introduced. Whatever input–output combination was used, the represented metric of the forearm was relatively accurate, and most important, comparable across conditions supposed to access different body representations. In the study by Newport et al. (2010), the authors showed a dissociation between BS and BI only on the extent of plasticity they were able to induce. Indeed, both representations were affected by the active version of the RHI, however, the extent of this modification, i.e., the number of supernumerary hands that was possible to incorporate, was not the same. The BI seemed indeed able to incorporate at least two supernumerary hands, while the BS appears to be more conservative, allowing the incorporation and motor control of only one hand.

To conclude, this study shows that tool-use can selectively update the BS when assessed by using appropriate combinations between the sensory modality of the input and the task modality of the output, revealing that a critical role is played by tactile information in updating the BS. Overall, these findings also suggest that although their functions are different, BS and BI are interconnected and might influence each other in physiological conditions depending, again, on the task the subject is asked to perform and the input–output modalities used to perform the task. Moreover, our findings reveal the BS contains a relatively accurate body metric. The present work thus constitutes both a confirmation of the theoretical implications advanced by Kammers and colleagues, and an interesting step forward of the theoretical framework they introduced: the importance of taking into account the input together with the output modalities is here applied to experimental paradigms for the study of body representation, which should extend beyond the situation of bodily illusion. The present results may also open new perspectives as to the study of body representation in brain-damaged patients (Berlucchi & Aglioti, 1997, 2010), whose almost exclusive approach in the past has focused the output side.

Declaration of conflicting interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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[1] We thank an anonymous reviewer for suggesting the tactile-perceptual input-out combination of experiment 3.

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The results of this study confirm the idea that the BS is a body representation essentially based on somatosensory information. Tactile stimuli only, and not verbal cues, were indeed effective in accessing the BS and showing its functional update following tool-use. The notion that the somatosensory system is the one that plays a key role in the building and construction of the BS was already present in the first definition of the BS. As I mentioned in the chapter 1, when Head and Holmes wrote "*the activity of the cortex brings every fresh group of sensations evoked by altered posture into relation with it [the posture]"* they clearly suggested that proprioceptive information are used by the brain to build and keep up to date the BS. However, with this study we showed that tactile information too contributes to the update of the BS. The importance of the somatosensory system in the construction of body representations is not difficult to understand. Through this system a constant flow of information reaches the cortex to inform the brain about the current state of the body and possible interactions with the external world.

The somatosensory system has also been proved to be modulated during action execution. Animal studies showed that direct stimulation of S1 produce detectable movements in mouse whisker of similar amplitude as those elicited by stimulation of M1 (Matyas et al. 2010). Welker and colleagues (Welker et al. 1957) showed that stimulation of postcentral areas of squirrel monkey brain also elicits movements which pattern of organization mirrors those of movements produced by stimulation of precentral areas. Seki et al. (Seki, Perlmutter, and Fetz 2003) also showed in monkeys that tactile stimulations were inhibited presynaptically to the level of the spinal cord prior to wrist movements. The authors suggested that this mechanism might be responsible for the increase in perceptual threshold during movements. In humans, it has been observed that while performing an action, the tactile threshold increases (Rushton, Rothwell, and Craggs 1981; CE Chapman et al. 1987) a phenomenon called sensory-motor gating. Rushton and colleagues (1987) described this phenomenon with a series of EEG studies that revealed the gating to be specific for the P45-N55 response only when the stimulated finger is the one that is used to perform the action and that the amplitude of the gating is proportional to the movement velocity (see also Angel and Malenka 1982). Moreover, the attenuation of tactile processing starts before the actual movement onset but does not last after its end (Shimazu et al. 1999; Rushton, Rothwell, and Craggs 1981). Voisin and colleagues (Voisin et al. 2011) recently showed that the sensory motor gating is present also in observation. The authors applied a continuous sensory stimulation at 25 Hz and studied the somatosensory steady-state responses (SSSR), which is a long-lasting electrophysiological brain response with which the stimulation shares the frequency, on subjects that were instructed to watch video clips of acting hands, feet, static hands, static objects and static hands passively stimulated. They found that only while watching video clips of a moving hand or a passively stimulated (touched) hand, the SSSR was reduced in average of 22% and 17% respectively. They interpreted this effect as the result of a tactile gating effect as the one observed during action execution. Kinematics studies also support the role of tactile and proprioceptive information in the motor control of grasping and reaching movements and in their online correction in case of a sudden and unexpected perturbation. In a series of studies initiated by Jeannerod's group, (Paulignan, MacKenzie, et al. 1991; Paulignan, Jeannerod, et al. 1991; M Desmurget et al. 1998; Gréa et al. 2002) it has been made clear that within a short delay after perturbation, subjects are able to correct their trajectory, or pre-shaping of their hand when object position, or size is modified. This online correction, of which subjects are not aware, is supposedly based on tactile and proprioceptive information that are compared to the motor plan that is elaborated before initiating the movement. This constant forward monitoring of motor execution, also enriched through sensory feedback, is not based on visual information, as visual pathways are not fast enough to assure a rapid correction. Indeed, when a lesion damages the somatosensory pathway, as in deafferented patients, the ability of rapidly correcting for perturbations is impaired (the motor performance of deafferented patients will be breifly discussed in the discussion session). Reach to grasp movements may actually be altered by relatively minor, acute somatosensory deprivation, as demonstarted by Gentilucci and colleauges when analysing the kinemtics of prehension movements performed by subjects after local anesthesia of the grasping index finger (Gentilucci, Toni, Daprati, & Gangitano, 1997). They found that movements performed under anesthesia were characterized by an increase of the maximal grip aperture and a lengthened early grip phase (the finger aperture phase) while the final part of the grip phase (the finger-closure) was relatively spared. This alteration of the grip phase induced also an increase in the variability of the transport phase. Taken together, these results speak in favor of the importance of tactile information in the control of fingers posture during prehension. Moreover, the effect on the transport component also supports the notion of the existence of a coordination between the grip and transport component.

A second main finding of study 2 concerns the relationship between BS and BI and the selectivity of tool-use effects. By using an appropriate combination of input and output, we have been able to go beyond this dissociation and show that these two representations are highly interconnected. Indeed, with the experiment 1 (tactile input-motor output) and 4 (verbal input-perceptual output), which were designed to be unbalanced toward one representation (BS and BI, respectively), we found a dissociation in the sense that only the experiment involving the BS showed the effect of the incorporation of the tool.

The fact that BS was affected by tool-use confirms that this representation is indeed involved in and integrates information relevant to action performance. On the other hand, the immunity of the BI, as shown by the perceptual task triggered by the verbal cues, or even by the results of the pointing task in the naming condition, supports the notion that this representation plays a role in perceptual tasks. Moreover, our results also show that the level of consciousness is an important criterion to differentiate between BS and BI, since the verbal access, which implies a conscious semantic elaboration of the to-be-localized body part, prevented the access to the BS, no matter the type of output task. Again, the unconscious nature of the BS was already present in Head and Holmes definition (see p. 13) and pervaded Gallagher's model of body representations (2005). According to this author, indeed, the availability to consciousness is one of the major axis along which BS and BI can be classified.

Evidence supporting the notion of consciousness as a discriminative criterion between BS and BI come from neuropsychological data. Rossetti and colleagues (1995) already proved the verbal output to be effective in disrupting the spared pointing capabilities of the patient they tested, which were based on an intact BS, when asked to point to a tactile stimulation. Indeed, when asked to verbally localize a tactile stimulation or to couple the verbal response with the pointing movement, the patient's performance was impaired, a result suggesting that the verbal output was rather accessing the BI, which was damaged in this patient. In our study, thanks to the new methodological approach we used, i.e. combining different inputs and outputs, we showed that the verbal modality implies the access to the BI even when used as input and coupled with a motor output (experiment 2).

The same approach also allowed us to show that, despite an independent existence of the two representations, BS and BI are also highly interacting.

Experiments 2 (verbal input-motor output) and 3 (tactile input-perceptual output) represent the intermediate positions between two extremes, allowing for the typical input of the BS (touch) to be assessed with the typical output feature of the BI (perceptual), and vice versa.

Experiment 2 showed that the increase in the participants' represented arm length depends on the type of input: After tool-use, pointing to verbally identified target landmark on the forearm was ineffective. Noteworthy, such a differential pattern emerged despite the very same motor pointing task as in experiment 1 was used and the same visual information about landmarks position was allowed before starting the open-loop pointing in each experiment. In experiment 3 we found a significant effect of tool-use on the represented forearm length, also in the direction of tool-incorporation. This result would not have been predicted by a merely output-based rationale: Considering only the output of the experiment 3 (a perceptual judgment), one would expect to find a result similar to the verbally triggered judgment of experiment 4. Moreover, this result seems in contrast with what found by Rossetti and colleagues (1995) and described above, that is the fact that localizing touch through a verbal response is not based on the BS. However, some differences exist between the studies: in Rossetti et al's work, the patient had to name the arm part she felt the stimulation on. This task stresses the perceptual-conscious aspects that are typical of the BI. At the contrary, in our task, the localization of the touch does not require a conscious elaboration of the body configuration and the reference to a conscious image of the body part. Indeed, the tactile stimulation can be mapped on an unconscious BS and then projected to a point in the external space independently from the creation of a conscious image of the arm. Thus, the verbal output is only the final step of localization process that takes place using the BS. As said for the pointing (p. 30 of this thesis, Milner and Goodale, 2007), the fact that the output is perceptual does not imply that the input information to perform the task is elaborated through a perceptual route or, in our case, essentially using a perceptual body representation.

Taken together, the results of our second study also support the importance of a methodological approach that takes into account both input and output modalities, as well as their interaction. Body representations are rich constructions that subserve many functions and rely on different sensory feedbacks. To limit the scientific approach to one aspect, as the perceptual/motor or conscious/unconscious dichotomy would be reductive, as suggested also by Kammers and colleagues (2010).

Finally, an issue that deserves discussion concerns the metric properties of BS and BI. We found that subjects, no matter the task they were requested to do, showed a tendency to underestimate the length of their hand and arm. Distortions in body representations size are present even in the early stage of somatosensory representations. Both the motor and perceptual homunculi consist of distorted maps of body parts based on a functional principle. For the somatosensory homunculus, the more sensitive parts of the body, as the lips and fingertips have a larger cortical representation than other, less sensitive parts, as the arms and the back, despite the actual physical size is smaller (Penfield and Boldrey, 1937; Penfield and Rasmussen, 1950; Nakamura et al, 1998). The distortion of primary maps is in some way compensated for by higher level representations, as shown by the fact that felt distances among tactile stimulations in different parts of the body do not reflect the same amount of error, although rescaling is not fully achieved as the Webber Illusion clearly demonstrates (Weber 1978).

Longo and Haggard (2010) recently quantified the distortion in the hand representation using a non-ballistic pointing toward named hand parts (see p. 47 for more details about the experiment). They found a massive overestimation of the hand width relative to its length. In particular, they found that the palm of the hand was estimated as being larger than its veridical size, while the fingers where represented as shorter than their real length. In our experiments, we also consistently found an underestimation of the hand length, ranging from 63% in experiment 3 (tactile-to-perceptual) to 79% of experiment 1 (tactile-to-motor). For the arm, the underestimation reached the significant level only for the two perceptual tasks. One possible interpretation is that the in the body schema, as tested through the point to touch task (experiment 1) would be more accurate for the arm in the distal-proximal direction than for the hand. This could reflect the functional characteristics of the two body parts in the motor context. For the arm, the relevant information is the length since its main function is to transport the hand toward a target object. Arm length is also the mostly relevant information to judge about the reachability of an object in the external space (Coello et al. 2008; M Longo and Lourenco 2007). For the hand, the distance between wrist and tip of the middle finger is probably less relevant than, for example, the relative distance between thumb and index finger, which is fundamental for a correct grasping. Since we did not test for the lateral direction of the distortion, we can only speculate about the fact that a more correct measure can be obtained when testing the hand width representation in the BS.

For the underestimation of the arm in the perceptual tasks, which are more related to the BI, the underestimation of the arm can reflect a lack of compensation of the somatosensory representation even at this high level of representation. When comparing the level of underestimation between the arm and the hand, the pattern of results is slightly different. Indeed, there is no difference between the hand and the arm for the two tasks triggered by the tactile stimulation, while in the two verbally triggered tasks the arm underestimation is significantly smaller than the one of the hand. This result is in line with spontaneous reports of the large majority of our subjects who consciously described their arm as much longer than the hand, than it actually is.

STUDY 3

Grasping with pliers vs. lengthened fingers induces different dynamic changes in the body representation

Cardinali et al.,(manuscript in preparation)

Once the plasticity of the body schema proven, the question about the specificity of the phenomenon arises. The human body undergoes impressive changes in length and weight during lifetime. The biological scaling, that is the change in characteristics of a body (human or animal) when its length is changed, is driven by two rules. Isometric scaling refers to the proportional concurrent change of different body characteristics, as in the case of height and body depth. In contrast, allometric scaling happens when body features increase by different percentages. For example, in human beings a 20% increase in height results in 73% of increase in weight (Samaras, Bartke, and Rollo 2007). This type of change is the most frequent for the human species, as well as for other animals, and it implies that disproportions in weight, size, depth and length increases exist. Consequently, the BS should be able to separately update the representation of different body parts according to their own timescales, for movement accuracy to be kept constant. Once again, tool-use seems to be the suitable paradigm to test this hypothesis. Indeed, we can think at tools that selectively modify one body segment and then study the effect on multiple body parts' representations. In the study n.1 we already showed that the use of a long grabber had a selective effect on the representation of the arm, as we found no modification of the grasping component of the movements performed after the training, while the transport component was systematically affected. We interpreted this effect as the consequence of the selective update of the arm representation due to the particular functional feature of the grabber used, i.e. to elongate the arm length. Here, we wanted to test whether using a tool that selectively modifies fingers features, and in particular the length of the thumb and the index finger, would led to a selective update of the hand kinematics, leaving the arm representation unaffected.

Using the same kinematic paradigm as in study 1, we designed a first experiment were we asked subjects to grasp an object before and after a short period of use of pliers. The pliers, which were opened and closed by the thumb and the index fingers, produced a functional elongation of the hand's grasping capabilities. We predicted a change in the grip component of the grasping movement performed after the use of the pliers, and not in the transport component. Moreover, by asking subjects to grasp objects also between thumb and middle finger (i.e. a finger not used during the training), we tested for the possible generalization of the effect to the hand.

In a second experiment, we addressed the question of whether inducing the same functional elongation of the same fingers (thumb and index) through a different device would lead to a different type of change in the subsequent kinematics. In particular, instead of using pliers, subjects were asked to grasp an object between sticks that were attached to their finger pads. In such a way, we were able to test whether the BS is sensitive to body-parts' growth, by mimicking it via an abrupt and temporary increase of the fingers' length. In addition, the comparison between the two experiments also allowed us to determine whether and to what extent the BS can make the difference between different sources of body modification. Although the two devices induced the same amount of finger elongation, and both had the same function, i.e. to grasp, they differed in the way they modified the fingers functioning. Pliers required to be operated by acting on a single object, which so-to-speak becomes the new functional grip of the hand. In contrast, sticks did not change the functioning of the fingers, but merely elongated them. By studying the kinematics of the movements performed before, after and during the use of the two devices, we aimed at addressing the question of whether and how different ways of modifying the functioning of the same effectors would results in a different update of the body representation for action.

Grasping with pliers vs. lengthened fingers induces different dynamic changes in the body representation.

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Introduction

The Body Schema (Head and Holmes, 1911) is a representation of our own body the brain relies upon to correctly plan and execute actions. Information about body parts' position and dimension, critical for correct motor control, are both possibly represented in the BS (see M Longo and Haggard 2010 for a different model). Tool-use can be an effective model for studying the plasticity of the BS, since it produces an abrupt change in body size that needs a quick and efficient update of the Body Schema. It also posits a great challenge to the sensorimotor system: during tool-use, not only the brain has to control the body to achieve the goal, but also an external object that it's temporarily attached to it. When we use tools, we don't always have time to explore them, or to deeply understand their mechanics or functional structure, and hopefully we don't need to know much about physics to proficiently use tools. For many, even relatively unfamiliar tools, we can just grab them and readily use them. How does the brain face the challenges that are left behind such an apparent ease of tool-use? It is believed that one key aspect may reside in the ability of the Body Schema to temporarily incorporate the tool in the body representation. This possibility implies that when we are using a tool the brain is processing it as an extended part of the body-part that controls it, at least from a motor point of view. This has two major implications. The first is that an update of the body representation should happen during tool use, and the second is that the update should concern only the body feature that is functionally modified by the tool.

We recently addressed the first point and we have shown that the use of a mechanical grabber, which physically and functionally extends the arm length by about 40 cm, results in changes affecting the way the brain controls the arm (Cardinali et al 2009). For example, we found that the kinematic profile that are visible in alterations of subsequent free-hand movements. For example, we found that after the use of the grabber, subjects performed free-hand grasping movements with delayed (in time) and reduced (in amplitudes) peaks of velocity and deceleration. We also proved that this effect was not due to muscular fatigue, since the kinematics did not change after performing the same amount of movements as with the tool, but with a weight attached to the wrist. Instead, it mimicked in direction the difference naturally present in individuals when there are compared on the basis of their arm length. In other words, the difference between pre and post tool-use was the same we found between subjects with a short arm or a long arm. Crucially, we found that only the arm behavior was modified, as testified by the fact that only the transport component of the movement (i.e. when the arm brings the hand in the vicinity of the target object) was different than before tool-use, and not the grip component (i.e. the preshaping of the fingers during the approaching to the object). In addition, kinematics of the transport phase was similarly affected when subjects were asked to point to the top of objects, instead of grasping them. As the tool was never used to point, we concluded that the dynamic update of the BS can generalize to untrained movements, provided that they feature the affected movement component (here, the transport of the hand toward the object). Overall, these finding suggest that using a tool as a grabber, whose functional addition to the body capabilities mainly consists of lengthening the reach possibilities, may produce a selective modification of the component that is more related to this feature.

The second point, however, has been until known untested and it is presently unknown whether different tools with different functional properties would differently affect the BS, an hypothesis one should put forward if the plasticity of the BS has to be thought of as being functional to skillful motor control in general, and tool-use in particular.

Here, we therefore tested the hypothesis that selective modifications in movement control after tool-use are a basic rule governing the dynamic updating of the body representation for action. In particular, we predicted that using a tool that mainly modifies the mechanical operativity of the hand will induce a selective modification in the subsequent control of the hand grip component, leaving the arm transport component relatively unchanged. In addition, on the basis of our previous findings, on the generalization to non-tool-trained actions, we tested the hypothesis that tool-use dependent changes in the hand kinematic would generalize to a type of finger-grip that was not involved in using the pliers.

To these aims, we analyzed the kinematics of healthy participants who were asked to perform free-hand grasping involving thumb-index finger-grip and thumb-middle finger-grip before and after using pliers to grasp a target object. The pliers had a simple two-fingered structure that overall lengthened the fingers length by about 8cm and could be used by opposing any finger to the thumb. However, during the tool-use phase, we constrained the subjects to operate the pliers by using only the thumb-index finger-grip.

In a second experiment, we further investigated whether the BS is sensitive to a similar change in the size of the fingers (also lengthened by about 8 cm) that was achieved, however, without the manipulation of a single functional tool. Rather, we mimicked an abrupt morphological increase of fingers by attaching two flat sticks to the distal phalanx of the subjects' thumb and index fingers. Similar to Experiment 1, both thumb-index and thumb-middle finger-grips movements were tested and compared before and after the use of the elongated fingers to grasp a target object. At variance with Experiment 1, the elongated fingers could not be acted upon by other fingers than those to which they were attached. In sum, pliers requires a functional use of an external tool that transiently changes the functional structure of the hand, whereas the elongated fingers were maneuvered more 'directly' to act upon the same target object. We therefore predicted that while both pliers and elongated fingers would selectively alter the kinematics of the hand grasping parameters, the use of the latter would not generalize to non-trained finger-grip, as proper tool-use (i.e., pliers) would do.

Materials and methods

Sixteen subjects (7 males, mean age 24 years; sd 3,7) participated to the study. None had previous history of neurological or psychiatric disorders and all had normal or corrected to normal vision. They were enrolled in the study, which was approved by the INSERM ethics board, after giving their informed consent. Two of them were left-handed and one ambidextrous as per personal report, and all performed the tasks with the right hand.

Subjects were comfortably seated facing a table with an A4 sheet of paper located horizontally in front of them. At its center, line drawings marked the contours of an object that, at each trail, could be positioned in one of two possible orientations.

The starting point for the grasping tasks (see below) consisted of two separated switches for the right and left hand attached to a wooden block that was firmly attached to the proximal edge of the table so that the distance between the right grasping hand and the target object was 22 cm. To record the kinematics of grasping movements an IRED (infrared emitting diode) marker was placed on each of four locations on the subject's forearm: the right thumbnail, the index and middle fingernails, as well as the styloid process of the wrist (see Figure 1). A high-resolution motion tracking system (Optotrak 3020, Northern Digital Inc., Ontario, Canada) was used to record markers' position over time (200 Hz).

Experiment 1 and 2 were both composed by a pre-tool-use phase, a tool-use phase and a post-tool-use phase. They only differed for the type of device subjects had to use during the intermediate phase. In the pre- and post-tool-use phases, subjects were asked to perform two different types of prehensile movements: thumb-index (T-I) finger grasping (12 trials) and thumb-middle finger (T-M) grasping (12 trials). The order of grasping type was counterbalanced across subjects.

Participants were asked to keep both hands in the pinch position, i.e. thumb and the finger-to-be-used in contact, on the starting switch, wait for the acoustical 'go' signal (a beep). All subjects used the right hand to perform all the three phases of each experiment. One of the experimenters positioned the object on the table inside the drawn contour and set off the trial. After a random delay, an acoustical go signal was presented and subjects had to reach to grasp the object between thumb and index finger, or thumb and middle finger, depending on the block. Then, they had to lift and replace the object inside the drawn contours and return to the starting position.

In Experiment 1 (Pliers) the intermediate phase consisted of using custom-made pliers to perform four blocks of grasping movements (12 trials each) of the same objects used in the pre- and post-tool-use phases. Pliers were made of a pair of 13-cm long plastic bands that were joined at one end (see Figure 1a) and subjects had to manipulate by using only the thumb and index finger. The remaining fingers were kept close on the palm of the hand throughout the experiment (see Figure 1a). Two spots were marked along the bands to indicate the place where thumb and index fingerpads had to be positioned to maneuver the pliers, which thus elongated the fingertips by about 8 cm. The starting position was the same as for pre and post tool-use phases, but subjects had to put the two distal extremities of the pliers on the switch (i.e., in the same pinch-grip posture). Object location was also the same as in the pre- and post-tool-use phases.

In Experiment 2 (Sticks), all the set-up and procedures were identical to those of experiment 1, except that subjects were using the flat sticks attached to their thumb and index fingertips to grasp, lift and replace the target object in the intermediate phase. The sticks were attached medially at the distal phalanx and taped to the pad in such a way that the extension produced on the fingertips was comparable to that obtained with the Pliers (i.e., about 8 cm).

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Insert Figure 1 here

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Movements were analyzed offline via a Matlab-based custom-developed software (Main) to extract the following transport and grip phases parameters: acceleration, velocity and deceleration of the wrist (the transport component of the movement); velocity of grip aperture (VGA) and maximal grip aperture (MGA) (for the grip component of the movement). For each of these parameters, two measures were extracted and analyzed: the latency, that is the time at which the peak of the parameter was reached, and its amplitude. The total movement time (MT) and reaction time (RT) were also studied.

Results

For technical problems due to the loss of visibility of an IRED marker, the VGA peak latency and amplitude could not be extracted for one subject in one condition (12 movements of TIG in the pre-training Experiment 1), which was therefore not analyzed for this parameter.

A three-way ANOVA with Experiment (Pliers vs. Sticks), Time (Pre vs. Post) and Finger-grip (T-I vs. T-M) as within-subject variables was run for all the kinematic parameters considered. Out of six parameters of the transport component, only the latency of the acceleration peak was significantly modified, as shown by a main effect of Time (F(1,15)=4,63, p =.04) indicating that the latency of this parameter was reduced in the post- as compared with the pre-tool-use phase. In contrast, all of the spatial, as well as the temporal parameters of the grip component were significantly affected. For the velocity of grip aperture (VGA), both in terms of its latency and peak amplitude, there was a main effect of Experiment (VGA Latency: (F(1,14), p=11.06, p=.01); VGA peak: (F(1,14), p=10.67,p=.01)) showing that in Experiment 2 (Sticks) subjects performed movements with overall longer latencies (309 vs 265 ms) and reduced peaks (364 vs 449 mm/s). Interestingly, there was also a significant main effect of Time (F(1,14), p=5.39, p=.03) for the VGA latency, which was reduced in the post-tool-use phases (post-tool= 278 ms; pre-tool= 297 ms), irrespective of both the type of device (pliers or sticks) and finger-grip (TI and TM). Moreover, for the VGA peak there was also a significant effect of Finger-grip (F(1,14), p=7.04, p=.02), T-M movements being characterized by higher VGA (424 mm/s) then T-I (389 mm/s). No significant interactions were observed for the VGA.

On the contrary, the ANOVA on the maximum grip aperture (MGA) resulted in a main effect of Time (Pre= 95mm, Post= 93mm; (F(1,15)=4.75, p=.04)) and Movement (T-I= 92mm, T-M= 96mm; F(1,15)=14.48, p<.01), as well as a three-way interaction between Experiment, Time and Movement (F(1,15)=5.04, p=.04). Planned comparisons revealed that after the use of the pliers the MGA was significantly reduced in the post-tool-use phase for both T-I (96mm vs 93mm; p=.02) and T-M finger-grips (99mm vs. 95mm; p=.03). As illustrated in Figure 2, however, after the use of the sticks the MGA was reduced only for the T-I (92mm vs 89mm; p=.02), but not for the T-M (95mm vs 95mm; p=.99). Finally, there was a main effect of Time for the Movement Time (F(1,14)=9.02, p=.01), showing that the total movement duration was reduced in the post-tool-use phases (716 ms vs. 675ms).

In the light of the differential effects attributable to the two devices on the subsequent free-hand kinematics, we ran an additional ANOVA with Experiment (Pliers vs. Sticks) and Block (First, Second, Third and Fourth block of tool-use) as variables to characterize the kinematics of the grasping with each device and also to ascertain the possible evolution of the motor behavior during training with each device. This ANOVA revealed a main effect of Experiment for all the latencies of the kinematic parameters considered, as well as for the MT (see table 1 for p-values). In particular, during the use of the Pliers all the peaks of both the transport and the grip component were significantly anticipated as compared to those observed during the use of the Sticks. Moreover, there was a significant effect of Block for the Velocity Latency (F(3,45)=3.37, p=,03). Post-hoc test revealed that this was due to a significant reduction of this latency between the first and the fourth block. A significant interaction between Experiment and Block was also found for the VGA Latency (F(3,45)=3.60, p=.02). Post-hoc analysis showed a significant difference between the first and the fourth block during the use of the Sticks (p<.01). As the amplitude of the same parameters did not differ, this seems to suggest a different organization of the movement. However, since the MT was also reduced during the training with the sticks (756 vs 680 ms, p=.01), we analyzed two additional parameters. For each movement we calculated the time of appearance of the Velocity Latency (%Vel Lat) and VGA Latency (%VGA Lat) on the MT. These parameters take into account the difference in MT and are indicative of the internal structure of the movement. Two-tailed t-tests revealed no significant difference for the percentage of Velocity Latency between Pliers and Lengthened fingers. However, the percentage of VGA was significantly smaller for the Pliers (Fingers: 32%; Pliers: 14%, p<.01) suggesting the two devices differed in terms of the way in which the grip component is scaled inside the movement.

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Insert figure 2 here

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Discussion

Each time we act with a tool that modifies the body morphology, the brain is able to quickly take into account this modification and adjust movement planning and execution to the new effector's features. This extraordinary capacity of our brain to update the representation of the acting body, i.e. the Body Schema (BS), has received empirical support only recently in a study where we showed that the kinematic of grasping and pointing movements performed after the use of a mechanical grabber is different than that observed when the same movements are performed just before the use of this tool (Cardinali et al. 2009). Crucially, the way kinematics was altered supported the long-standing hypothesis that tool-use may cause a temporary incorporation of the tool (a 40cm long grabber) in the arm representation. Here, we provide a considerable advance to our understanding of the plasticity that is induced by tool-use as we start revealing what are the rules according to which this plasticity is achieved. In this respect, the present study contributes two major findings: First, tool-use-dependent plasticity is selective for the part of the effector that is concerned by the use of the tool, as both pliers and sticks altered the subsequent free-hand kinematics, but only for the grasping phase of prehension movements. Second, this plasticity reflects the nature of the functional change exerted on the effector, as using sticks had highly selective effects on the kinematics of the lengthened fingers, without affecting the adjacent finger, whereas using pliers brought to a more pervasive effect that generalized to a type of finger-grip that was not involved by this tool. These findings will be further discussed below.

As first result, we showed that the BS selectively updates the representation of those body segments that are directly modified by the device used to act. Indeed, we asked subjects to use devices that modified the fingers length and we found a selective effect on the grip component parameters of the movements, but the transport component was largely unaffected. Indeed, only the VGA and the MGA were affected after the use of the two devices and in particular we found a reduction of both the latency of the VGA and the amplitude of the MGA in the post tool-use phases. These parameters are related to the hand representation as they consist of the pre-shaping of the fingers (Jeannerod, 1981; 1984) thus suggesting that only the hand representation and not the arm has been updated by using pliers and sticks. It might be tempting to argue that the reduction of the MGA after the use of this tool may suggest that the hand is represented as bigger. While this possibility remains largely speculative, some empirical evidence from related works is worth considering. Marino and colleagues (Marino et al. 2010), for example, investigated the effect of planning and executing grasping actions under visual conditions in which the visual feedback originating from the subjects' grasping hand was modified on-line. When healthy participants performed reach to grasp movements while their hand was made to appear bigger than it really was, the kinematic analyses revealed that they adjusted their finger pre-shaping in the direction of a reduced MGA. In other words, grasping objects with a visually larger hand, made the subjects to downsize the most important spatial parameter of the grasping component, a finding similar to what we have reported here after the use of both the pliers and the sticks. Similarly, Karok and Newport (Karok and Newport 2010) recently tested a group of healthy subjects in a grasping task were visual feedback about either the hand or the object size was altered. They showed that when a gradual and continuous modification of the visual feedback about the hand was introduced, in the direction of enlarging its size, subjects' kinematics showed a reduced MGA. Altogether, these findings clearly point to the possibility that whether the hand is visually, or 'motorically' enlarged, the consequences on its motor control could be similar.

The second result is the different effect that the two devices we asked the subjects to use had on subsequent free-hand movements. We found that after the use of the sticks, only the movements performed with the elongated fingers were modified, while the use of the pliers induced a similar, although generalized effect on both types of finger grips. Critically, attaching sticks to the thumb and index finger did not provide a functional object to be operated by the hand: rather, it mimicked natural growth aspects, were the independence of the fingers was maintained

This updating of the hand representation for achieving the control of the tool reminds of "motor equivalence", one of the key properties of our motor system by which the same action goal can be performed by different effectors with basically the same movement pattern (Wing 2000; Keele, Cohen, and Ivry 1990; Lashley 1930). Although the action performed (to grasp) is the same with the pliers and the lengthened fingers, the way the action is implemented differs since the structure of the effector is not the same. This implies that the BS then has to build a representation of a new effector, and in particular of an effector composed by only two opposing "fingers", the thumb and a second finger, articulated on a single joint at the back of such fingers. Such a pervasive update of the BS is reflected in the kinematic of both types of finger-grips (thumb-index as well as the untrained thumb-middle), since they both involve the opposition of the thumb and a second finger. Motor-equivalence alone, however, is not sufficient to account for the full pattern of results. Despite the fact that the two devices produced the same amount of fingers elongation and were used for the same purpose, their kinematic profile was different. Indeed, when subjects were maneuvering the pliers, the temporal coupling of the transport and grip components suggested that priority was given to the latter, as shown by the early occurrence of the velocity peak of fingers aperture. In their model of motor schemas, Jeannerod and colleagues (1995) postulated that the time given to the two components of a prehension movement (transport and grip) can vary and is decided by a co-ordinating schema, according to the following principle: the component that will take longer to be completed will be prioritized and receive the time it needs. Here, the shorter latency of the peak velocity of finger aperture suggests that the grip component was given priority when using pliers, as compared to sticks, which may relate to the asymmetry in the generalization effects, present with pliers, absent with sticks.

To conclude, this study demonstrates that tool-use-dependent plasticity of the Body Schema is highly selective. Not only the dynamic updating concerns specifically the effector that operates the tool, but also relatively subtle changes in the way the effector functionality is altered are remarkably reflected at the behavioral level. Although this finding is not in itself a direct demonstration that skillful tool use depends upon the plastic features of the BS, it clearly supports the critical role the BS plays in the mastery of tools.

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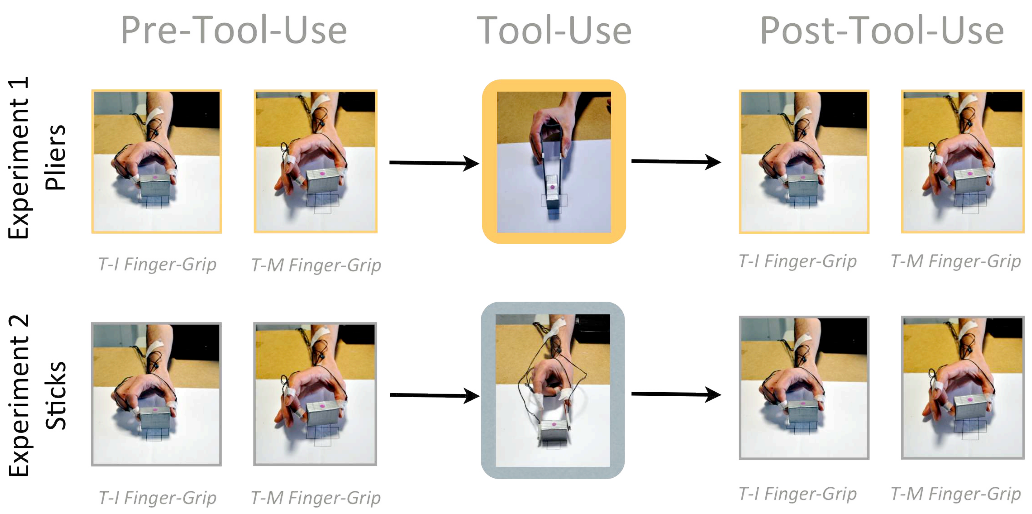

Figure 1. Experimental setup and time-course.

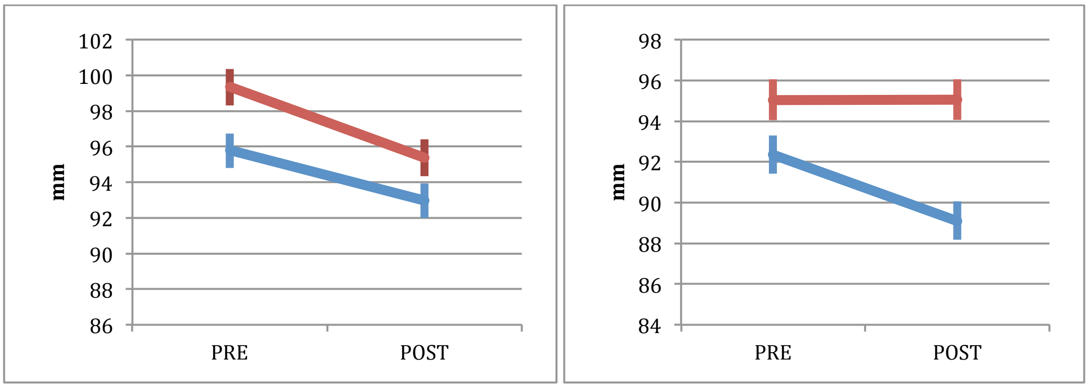

Figure 2. Results. MGA peak before and after tool-use for T-I finger-grip (Blue line) and T-M finger-grip (Red line) in Experiment 1(Pliers; left panel) and Experiment 2 (Sticks; right panel). Bars indicate S.E.M.

With this study, we made an important step forward into the knowledge of the rules that govern the plasticity of the BS. Together with the results of the first study, these data show that only the representation of the functionally modified body part is updated, and in a highly selective way. In both studies we asked subjects to grasp an object with their right hand before and after the use of a tool. When the tool used was a mechanical grabber, whose functional property was to elongate the arm, we found a modification in the kinematics of the transport component of the movement only; when the training consisted of using a device that functionally modified the hand grip, the effect on the kinematics of subsequent grasping movements was restricted to the grip component. As already shown in the chapter about the kinematics, these two components are related not only to different properties of the target object, but also to the representation of two different parts of the body, and in particular the arm for the transport and the hand for the grip component. The fact the only one component, and not the other, is modified inside the very same prehensile movement strongly supports a selective update of one body part only.

Moreover, it suggests that the BS does not follow a criterion of plausibility. Indeed, in both study 1 and 3 we induced a modification of the body that was, not only selective for one segment, but also abnormal if considered the standard size of a human body. Moreover, even when considering the amount of increase in size of a human body during the entire life, we must remember that such changes happen in a very long timescale. At the same time, tools are often built and used to overcome body limitations, thus permitting to do what would not be possible with an unmodified body. It becomes then important, for the body representation for action to be able to accept this type of “abnormalities”, given the importance and frequency with which we use tools in our daily life.

However, at p. 43-44 we discussed the results of Newport and colleagues study with the RHI paradigm and their discovery of a stronger coherence of the BS, compared to the BI, since this representation did not allow the incorporation of two replicas of the subject’s hand. Incorporating a supernumerary fake hand can be as abnormal as the fact of having an arm lengthened by 40 cm, or fingers as long as 15 cm. Why then it is acceptable for the BS to have an arm twice as longer than usual, but not two right hands? In one case the motor control is possible, since the tool can be maneuvered, while in the other case there is no real experience of exerting motor control over two right hands[8]. This observation can appear trivial, however it implies at least two consequences. On one hand, this adheres to the action-devoted nature of the BS. In this particular representation, what is represented is the action effector, no matter if it is a body-part or an external object. The second main consequence is that tactile and proprioceptive feedbacks play a key role in the update and maintain of the BS. Since we can have visual experience of our own body/effectors as well as of those of other people, the sensorimotor system is ideally placed to provide the brain with the necessary information to disentangle whether the hand/tool I see is my hand/my tool or not. Both aspects will be further discussed in the conclusion section.

Finally, Gallivan and colleagues (Gallivan, Cavina-Pratesi, and Culham 2009) used slow event-related fMRI to study whether the cortical area involved in reaching control during prehension (in particular the Superior Parietal-Occipital Cortex, SPOC) is differently activated by the presentation of objects close (reachable) or far (not-reachable) from the hand that is used to act. Of interest here is that in one of the experiments, they introduced a tool-use condition where subjects were asked to reach-to-grasp the target object by using pliers. By comparing the free hand and the tool condition, they found no differences in the SPOC activation. This result seems in line with our behavioral finding that the use of pliers has a selective effect on the hand representation and the grip component of the movement, and not on the arm representation (transport phase of the movement).

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[8] The supernumerary limbs phenomenon, where subjects vividly experience the presence of a third arm or hand, has been explained as a disorder related to the BS (Heed and Röder, 2011). Interestingly, this phenomenon is often associated with a paralysis of the corresponding real limb.

DISCUSSION AND PERSPECTIVES

General Discussion

We usually do not realize how important is to be able to correctly move, except when for some reasons, we are not allowed to do so anymore. The precision and ease with which we act in our environment is such a common experience that we are actually surprised when it is no longer the case. Let's imagine a simple situation in which we are about preparing a meal. We move around the kitchen, we grasp different types of objects, we act on them and with them on other objects and we don't feel like we are doing anything special. However, behind this ease of motor control of our body and tools there is an important and sustained effort of our brain that has to deal with many, continuously changing variables. First of all, the objects we want to act on. Are they heavy or light? Are they fragile or not? But also, are they close enough to be grasped or do we have to move? Then, there is the question about what we want to do: do we want to grasp, for example, an egg or do we want to open it? Of course, none of these questions are consciously asked, but instead we usually experience fluidity and ease when we act. At the cerebral level, even a simple action like reach out to grasp an object requires the involvement of an extensive circuit. We can identify three large nodes that are needed to accurately move. One is the processing of object related information, the second is the space representation, the third the action planning and execution. These processing are coded by highly integrated circuits in order to achieve the desired goal. They all have been deeply studied by researchers in the past years and their functioning is the more and more clear in our knowledge.

We know that different object characteristics are analyzed in specific pathways in order to extract information useful to guide actions. As described in the introduction to this thesis, a two-route model has been proposed in the past years to explain how the brain differently processes objects when they are targets of an action. The neural correlates of this model are quite well established. In particular, it has been proposed that the "how (to-act-on)" stream originates in the occipital cortex and moves along the parietal cortex where information, like the size or the position of the target, are processed and made available to the grasping circuits. Space representation is also shaped by the action intentions of the subject. It has been shown in monkeys, as well as in humans, that a particular region of space called Peripersonal Space serves and is shaped by action execution. Objects in this region, inside which tactile and visual/auditory information about an object are highly integrated, become particularly relevant to the subject's sensorimotor systems. Although the Peripersonal Space has a limited extension in depth, its boundaries have been proven to be flexible, so that when a subject plans an action toward a distant object, the multisensory processing of information coming from the to-be-grasped object and the grasping-hand is enhanced, possibly to guide the action execution.

Finally, the grasping circuit in human has also been extensively investigated and previous studies have shown that, besides the motor cortex, it involves the inferior parietal lobule, as well as more frontal regions like the ventral premotor cortex. However, something is typically missing in these motor-control based findings: the body. Indeed, the movements we plan at the end of all these processes will be implemented in an effector, which can be either our own body or an external object. From an embodied perspective, it is not possible to think about a grasping movement or imagine one without a corporal effector. At the same time, the selection of the movement to perform is also strictly dependent on the type of effector available. Once the goal to be achieved selected, the choice of the movement to execute will depend on the effectors available and the choice of the effectors will depend on what type of movement is more suitable to achieve the goal. Let's go back to the previous example and imagine you want to get the last drop of jam at the bottom of the pot. We can either do it with our own finger or decide to use a spoon. Besides the influence from other contextual constraints (i.e., whether you're alone in the kitchen or at a formal dinner at your boss' house), the decision will depend on the size and shape of both the pot and our own hand and the implemented movement will be different and it will be coded on the basis of the effector to be used. The inverse is possible too, that is to choose the effector on the basis of the desired action. For example, if you now want to throw the pot in the garbage bin, you will find that your own hand is a pretty good effector to do this, thus you probably won't need to use any tool. In most of cases, action planning and execution cannot disregard the body (as well as its substitutes) representation.

At the same time, once the motor schemes are recruited, the movement is implemented in one specific effector through commands that are directed to specific muscles. This implies that, at some point, the effector is chosen and its characteristics computed, or retrieved. The aim of my thesis has been to test the representation of the body that is used for action, which is known as Body Schema. In particular, the main goal was to test a very old hypothesis according to which the BS is a highly plastic representation that is capable of incorporating tools when these are used. To this aim, I used a very simple tool-use paradigm coupled with a behavioral approach to the study of movements that has a long history, namely kinematics.

The first main result obtained has been to provide empirical evidence in support of the popularly known and widely accepted notion that when we use an external object as a tool to perform actions, this object becomes a part of our own body (representation).

For a very long time, researchers have assumed as demonstrated the incorporation of tools in the Body Schema. I already argued in the introduction and in my theoretical contribution, how many studies (erroneously) interpreted modifications in space representation or perception as plasticity of the BS. It is still common to read papers in which terms like Body Schema and Peripersonal Space are used as synonymous, or where changes in multisensory integration in space are explained as an update of the BS. Although I do not exclude the possibility that a change in the BS (for example via tool-use) can lead to a concurrent update of the Peripersonal Space, the contrary has not yet been reported, to the best of my knowledge. As such, it is important to refer to each representation in the most appropriate way. I believe the results of my thesis offer in this confused framework an additional, methodological value. Indeed, we not only provided the first evidence of the plasticity of the BS, but we also developed a methodological approach adapted to the study of this representation. We indeed proved the output-dependent approach to be not sensitive enough to capture the plasticity of the BS, as well as its relationships with the BI.

As a second result, I provided strong support to the notion that the BS is an action-devoted representation, since it provides a representation of the body for action and, at the same time, it is shaped, modified by the action. I showed that the plastic changes that happen in the BS during, and are still visible after tool-use, strictly depend on the functional features of the used tool. In Study 3, we clearly demonstrated that what is relevant for the BS is the functional structure of the effector and its update will take into account those particular, even subtle features of the tool. I suggest that an operational definition of the BS should describe it as a repertoire of effectors. This updated definition strengthens the action-devoted nature of the BS and also takes into account the need to extend this representation beyond the body limits.

Also, we proved that touch provides a preferential access to the BS and its plasticity. But this raises questions as to whether, and to what extent, the pointing to touched body parts paradigm genuinely reflects the content of the BS and its plasticity, or at least whether it reflects it without the possible contribution of another metric, coming from possible interactions with the Body Image. This question, however, is to be addressed in another thesis!

Future perspectives

We recently addressed the question of the role of proprioception in the plasticity of the BS by studying tool-use in a deafferented patient, C.D., with a peripheral deafferentation of the right arm. In three separated sessions, we asked C.D. to grasp an object with both her right (deafferented) or left hand and a mechanical grab. We then analysed her kinematics. In the first session, we found that, differently from healthy subjects, double peaks of acceleration and velocity characterized the kinematics of the deafferented hand, suggesting that vision can only partially compensate for the lack of proprioception. Remarkably, the same double peaks kinematic profile was present when the same hand was controlling the tool. Moreover, the patient showed a relatively fast process of learning in using the tool, since the kinematics evolved during the too-use phase and crucially in the last block of trials with the tool, C. D. did not show double peaks anymore, but a normalised kinematic pattern with single velocity peaks, similar to healthy subjects.

In the post-tool-use, the newly acquired behaviour of the deafferented hand was fully transferred to the free-hand grasping that did not show double peaks anymore. The improvement in the motor performance is stable, since it was still visible in the second and third sessions that have been recorded 6 months and 2 years after the first testing session. Moreover, once the new normal profile acquired, the patient also showed the effect of the tool incorporation into the BS, i.e. the kinematic change for grasping movement consisting of longer latencies and reduced peaks amplitudes for the parameters of the transport component. Taken together these results suggest that vision can play a substitutive role when proprioception is no more available for updating the BS. However, this implies a process of learning in the use of the tool that was not observed in normal subjects, meaning the compensation is not immediately complete.

Incidentally, it is very interesting to observe that tool-use appeared to be an effective way to improve motor control in this patient, with long-lasting effects. This phenomenon, totally serendipitous, may well have implications in the rehabilitation domain of great relevance, and deserves further investigations.

A second point that deserves further investigations is the neural substrates of human skilful tool-use. Although modern neuroimaging has begun to address the brain circuits underlying tool use by studying neural activation for pictures of tools and pantomimed tool actions, almost no research has studied *real* tool use and its effect on the neural representation of the body. One of the possible reasons is that neuroimaging techniques, particularly fMRI, have only a very constrained space in which the research participant can act and are vulnerable to artifacts resulting from head or even body movement. As already mentioned before, a 2006 meta-analysis called, “Cortical Networks Related to Human Use of Tools” (Lewis, 2006), reviewed 64 paradigms from 35 studies that investigated tool naming, tool pantomiming, imagining tool use, viewing tools and hearing tools; notably, it included only one study that actually involved real use of a single tool, a pair of chopsticks (Inoue et al., 2001) and that study used positron emission tomography (PET) rather than fMRI. While PET is resilient to motion artifacts, it has many limitations, including relatively low spatial and temporal resolution compared to fMRI. It would been interesting then to study the plasticity of the BS with fMRI by asking subjects to actually use different tools in the scanner so to reveal the neural correlates of the BS and in particular of the selectivity for the body part I showed with my behavioral experiments (study 1 and 3).

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