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.

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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

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	Body knowledge for action
	Voluntary actions	
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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