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Introduction: Parts, body and the self

The body is made up of parts. This basic assumption is central in most neuroscientific studies of bodily sensation, body representation and motor action. Yet, the assumption has rarely been considered explicitly. We may indeed ask how the body is internally segmented and how body parts can be defined. That is, how can we sketch the mereology of the body? Mereology (from the Greek *meros*, 'part') is the theory of parthood relations: of the relations of part to whole and the relations of part to part within a whole. Traditionally, it addresses the metaphysical question of the relation between constitution and identity: is the sameness of parts *necessary* for identity? One of the most famous examples is the story of the cat Tibbles who loses his tail. If a cat survives the annihilation of its tail, then the cat *with* tail (before the accident) and the cat *without* tail (after the accident) are numerically the same in spite of their having different proper parts (Wiggins, 1980). Therefore, the cat cannot be identified to the corresponding amount of feline tissue, even if it is constituted by it. As Wiggins (1968, p. 90) said, "No man is the same as his forearm.".

In this chapter, we will not raise the metaphysical issue of personal identity, even if, as for Tibbles, we will mention the possibility of deletion of body parts. Rather, we are interested in the epistemological and phenomenological dimension of mereology of the body. Is somesthetic experience linked to body parts, or to the body as a whole? How are those parts to be described, and how do they relate to each other? Can the way I experience my body as a whole be reduced to the way I feel each of my body parts?

The body that we experience cannot be fully reduced to a bundle of tissues and organs. As Merleau-Ponty (1945) noticed, the body is an object that never leaves me. While we can perceive an object from different perspectives or cease to perceive it, we experience "the feeling of the same old body always there" (James, 1890, p. 242). The amount of information received on one's own body is quantitatively superior to what one can receive from any external object: not only can one see or touch one's own body, one also always receives a continuous flow of proprioceptive and somesthetic inputs. The embodied self is thus constructed from sensory inputs, but still cannot be reduced to the representation of coextended limbs. In addition to simply pooling information from different senses, body representations also synthesize the various signals into an integrated meaningful experience by establishing consistent relationships between body parts and the whole.

The simplest scientific approach to bodily experience is a reductive one. We begin by assuming that the phenomenology of the perceiving and acting body is not a primitive fact, but can be analysed. We approach this analysis by considering how the phenomenology of the body can be broken down into a phenomenology of body parts. This approach allows us to investigate the "embodied self" by reviewing how recent experimental data address three intimately related questions about body mereology: (1) what is the relation between the body parts and the body as a whole? (2) how are the various sources of information from different body parts combined to form a coherent body representation? (3) what is the relation between the body and the self?

1. **The mereological organization of the body**

We can perform actions without having first to direct attention to the position of our limbs. One might therefore assume that the continuous flow of information about our body that we use in action is always present to consciousness: we would always be aware of the body in all its details (O'Shaughnessy, 1980). However, many experiments have shown that actions are often performed outside the conscious field (Jeannerod, 1997), and do not require conscious representation of body position. For instance, Castiello, Paulignan, and Jeannerod (1991) showed that an unexpected target jump becomes available to consciousness 200 ms after the sensori-motor adjustment. It has also been demonstrated that we tend to adhere to the goal and not to the way it has been achieved (Fourneret & Jeannerod, 1998). In fact, it seems that the body remains most of the time at the margin of consciousness as an undifferentiated whole (Gurwitsch, 1985; O'Shaughnessy, 1995).

On the other hand, we can also allocate specific attention to one part of the body, either voluntarily, or because we are attracted by the saliency of a bodily sensation. Itches, pains and other bodily sensations can seem very focal indeed, popping out compellingly from the background experience of the body. This focality suggests that the localization of bodily sensations shows special characteristics. Bodily sensations appear to be encoded in a specialized somatotopic frame of reference, which we call "body space". Body space is characterized by the fact that it is quite distinct from external spatial locations. Body space can be interpreted as the mental map of the spatial disposition of body parts and of the relationship between the various parts of the body and the whole. It has to be distinguished from external objective space: a painful body part can move relatively to the external spatial framework without the pain itself moving within the body space. For instance, the pain in my thumb is not felt in my mouth just because my thumb is in my mouth (Block, 1983).

> The outline of my body is a frontier which ordinary spatial relations do not cross. (Merleau-Ponty, 1945, p. 98)

Consequently, we can ask about its internal mereological organization: how is the body segmented into parts?

Differentiation of body parts

One of the main problems of mereology is to define the relevant parts of the object. We single out the handle of the cup as a proper part because of its functional role, but we could as well decide to isolate another part on purely spatial criteria such as the base of the cup. The same problem thus arises for the body: how to differentiate the relevant body parts? Representations of the body can be segmented at different levels: sensorimotor, visuo-spatial and semantic (Sirigu et al., 1991). We suggest that body parts could be analysed in either of two different ways, through qualitative topology and quantitative geometry. Topology means differentiating the whole body into categorically distinct parts (e.g., 'arm', 'finger'). Geometry means differentiating the body into zones with metric properties such as extent. In this section, we begin by showing that topological mereology of the body differs according to whether sensory or motor aspects of the body are considered. We next consider the mental representation of geometric relations among body parts.

Somatosensory mereology

The body surface may be viewed as an undifferentiated tactile sheet, without categorical divisions corresponding to anatomical body parts. The connectivity between neurons in the cerebral cortex is responsible for imposing an ordered structure on this undifferentiated sheet. The different adjacent regions of the tactile sheet compete with each other to "own" cortical representation, by an ongoing process of lateral inhibition between cortical neurons, limiting the spread of excitation among adjacents neurons, thereby functionally isolating cells that are anatomically near each other. A structured map arises because specific patterns of lateral inhibition emerge during sensory experience. Indeed, primary somatosensory representations do generally follow the natural anatomical divisions of body parts, having receptive fields confined to single fingers or limbs (Penfield and Rasmussen, 1950; Blankenburg et al., 2003). Penfield and Boldrey (1937) described the somatotopical organization of SI that associates cortical areas to a part of the body surface resulting in the metaphor of a "Homunculus". However, this body-part based organization does not imply that the body is naturally differentiated into categorical parts at the level of primary representation. The structure of the homunculus is not a necessary property of the network wiring, but the result of plastic changes in tactile input altering the inhibitory competition between neurons. Differentiation into distinct body parts at the primary somatosensory level may be a reflection of how our bodies have been used, rather than a natural unit of neural representation.

It is only at a more cognitive level that the body space is properly differentiated into distinct body parts. The criteria of such differentiation are not fixed and may vary according to the function of the body representation. Again, the brain's differentiation of somatosensory input into body part categories is not innate, but may reflect the pattern of sensory inputs generated by our interactions with the environment. Mereological organization of the body representation should thus be influenced by tactile experience. Indeed, paired associative stimulation of adjacent digits produces confusions between the trained digits in identification tasks (Braun et al., 2000), and an increasing overlap between their cortical representations (Schweizer et al., 2001). Neuropsychological conditions such as finger agnosia suggest that poor differentiation of adjacent body parts can occur at a more cognitive level without deficit in primary sensation. For example, Kinsbourne and Warrington (1962) suggested that the ring and middle digits lose their separate identities in finger agnosia. Their representations become functionally fused. A similar line of argument may explain the errors made by autotopagnosic patients in pointing to body parts (Odgen, 1985, Sirigu et al., 1991). Patients may point either toward the contiguous body part (the wrist, rather than the hand) or to the contralateral body part (right hand rather than left hand) (Semenza, 1988).

We suggest that differentiation of the body into parts may reflect a competitive process of mutual inhibition occurring at the cognitive level of body representations. This could, for example, be a more abstract version of the competitive inhibition process between receptive fields known to exist in primary somatosensory representation. Nevertheless, this differentiation does not preclude, but rather highlights, the mutual relationship between parts that constitutes the body as a whole. Studies show indeed that the overall spatial configuration between the limbs plays a central role in body representations. The inversion of body parts affects the recognition of the body, while it would not influence the recognition of physical objects (see Reed, this volume). Interestingly, the inversion effect

can be elicited only if the biomechanical posture is motorically possible (Reed et al. 2003). This result points out the importance of a motor representation of the body.

<u>Motor mereology</u>

Any object may be broken down into constituent parts based on spatial information. However, our own body is a unique object because we can move it voluntarily. Therefore, body mereology may thus differ from other objects because my voluntary actions may provide an organizing principle for segmenting the body into parts. Interestingly, a motor mereology begins with a different spatial object from a somatosensory mereology. We have already described the somatosensory body surface as an undifferentiated sheet. In contrast, the starting point of motor mereology would be the set of muscles that I can voluntarily move. This is a group of different objects, rather than a continuous sensory organ. Furthermore, intentional actions impose an additional functional organization because of the sets of body parts that work together in intentional movements. For example, when I move my forearm my hand and fingers follow. In contrast, if someone touches my forearm, this usually does not tell me anything about the sensation in the hand and fingers. Accordingly, the representations in primary somatosensory cortex (SI) and primary motor cortex (MI) have quite different organizing principles. Although both have comparable gross somatotopy, fine somatotopy differs sharply between the two areas. While the receptive field of each neuron of SI corresponds to a small well-defined part of the cutaneous surface (Blankeburg et al., 2003), MI representations of the different body parts strongly overlap. MI seems to be organized for representing muscle groups and patterns of movement rather than individual muscles (Lemon, 1988). Furthermore, accumulating evidence suggest that somatotopical organization in SI allows for additive activation, such that the corresponding cortical volume of the movement of three fingers is the sum of the volumes for the individual fingers moved alone (Hlustik et al., 2001). This does not seem to be the case in MI:

> where the 'sum of the parts' is qualitatively different than the sum found for SI.[…] MI and SI share a common somatotopic principle but the somatotopy in SI is more discreet and segregated, in contrast to the more integrated and overlapping somatotopy in MI. (Hlustik et al., 2001, p. 319)

The pattern of activation in MI suggests that the control of any finger movement recruits a population of neurons distributed throughout MI, rather than a segregated population that would map point-to-point distinct movements based on a somatotopic organization (Schieber & Hibbard, 1993).

INSERT FIGURE 1 AROUND HERE

A more conceptual way of thinking about body representation may suggest that action plays an important role in imposing categorical structure on body space. In particular, we act around our joints and these become body part boundaries. While there seems to be no specific natural boundaries for the somatosensory body, we may suggest that the joints constitute the landmarks for segmenting the acting body:

> Individual body parts are paradigmatically identified in terms of hinges. The forearm, for example, is the volume between the elbow and the wrist (…) Using hinges provides a non arbitrary way of segmenting the body

that accords pretty closely with how we classify body parts in everyday thought and speech (Bermudez, 1998, p. 156)

The topological mereology of the body seems immediately present even in primary representations for action, while in the somatosensory system mereology seems to emerge only at a more cognitive level.

<u>The size of body parts</u>

Body mereology has qualitative and quantitative aspects. While body topology concerns the boundaries between body parts, body geometry refers to metric relations such as the relative size of body parts. Information about body part size is essential for planning and control of action: for example, if I want to switch on the light, I need to know the length of my arm in order to decide whether I can reach the switch without getting up from my chair. The afferent somatosensory and proprioceptive systems do not provide any direct information about body part size. Moreover, the body maps in primary somatosensory cortex are highly distorted: physically small areas of skin such as the fingertips having much larger cortical territories than large body parts such as the upper arm or back. Several studies suggest that the perceived size of body parts reflects mutual interactions between these underlying neural representations.

First, Gandevia and Phegan (1999) suggested that the perceived size of body parts may be modulated by afferent inputs. These authors asked subjects to draw their lips and thumb at their currently perceived size, while either of these body parts was temporarily anaesthetized. The lip and the thumb were chosen because they are represented in a common region of primary somatosensory cortex. Anaesthesia increased the perceived size of the anaesthetized body part, and had a similar but smaller effect on the other unanaesthetized part. The transfer from the anesthetized to the unanaesthetised part was attributed to the shared cortical representation of the hand and face. This result suggests that the cognitive representation of the body is driven by integrating over regions of the primary cortical map.

Taylor-Clarke et al. (2004) investigated how the tactile perception of a stimulus depends according to the body part that is touched. Subjects compared the distance between two points touched on the index finger with a second distance presented on the forearm. Subjects perceived tactile distances on the finger as larger than identical distances on the forearm, presumably due to the relative imbalance of the cortical territories of these body parts. However, this effect was significantly reduced after subjects merely *viewed* a distorted image of their body in which the hand was reduced and shown at the end of an enlarged forearm. A visual representation of the volumetric size of body parts provides the spatial information required to interpret tactile stimuli. This result suggests that the neural representation of tactile information local to each body part depends on an internal body model in which the size of each part is represented. This body model is driven at least partly by vision, and defines the mereological composition of the body.

Lackner (1988) showed that the internal body model also receives proprioceptive inputs. He induced illusory perception of the size of body parts by vibrating the tendons of arm muscles. Such vibrations induce illusory arm movements. Subjects were required to grasp their nose during the vibration. Subjects reported that they experienced their nose as elongating by much as 30 cm. This "Pinocchio illusion" constitutes the solution of a

sensorimotor conflict: the vibration gives the illusion of arm extension, but the fact that the hand maintains contact with the nose means that the nose is also moving. Since the head and the body are stationary, the combined sensory input is interpreted as the nose elongating. Body parts are thus represented in their mutual mereological relationship and the representation of the body cannot be reduced to independent representations of each body part. Therefore, the configuration of the whole body is "inferred" from the various inputs, rather than directly perceived. The body scheme results from the interaction between the different body parts and the different sensory modalities

INSERT FIGURE 2 HERE

Taken together, all these studies suggest that the geometric mereology of the body is fundamentally a product of multisensory integration. The spatial representation of the body depends on the integration of tactile, proprioceptive and visual inputs. Vision may play a special structuring role, by imposing a metric organization based on bounded body parts on a relatively continuous sensory sheet.

Addition and deletion

Illusions of body part size show that body space does not constitute a complete and accurate display of the body in our mind. Furthermore, the borders of body space do not always coincide with the actual limits of the physical body. Several kinds of neuroscientific data clarify the body concept by describing the neural mechanisms and psychological consequences of deletion and addition of body parts.

<u>Deletion</u>

Amputation provides the most obvious example of body part physical deletion. It is accompanied by major cortical reorganization giving rise to "phantom" sensations which feel as though they originate in the absent body part. Thus, light touch on the face area contralateral to the amputation elicits somatotopically mapped sensations on the phantom limb (Ramachandran and Ramachandran, 1996). This effect is thought to arise because cortical regions previously representing the amputated body part become responsive to stimuli on the face after amputation, yet the subjective sensation correlated with the neural activity retains the feel of the phantom (Ramachandran and Hirstein, 1998). Studies of rapid reorganization of tactile neurons following amputation in animals suggest that these sensations arise because cortical neurons which represent the body receive afferent input from several body parts. A process of lateral inhibition between inputs ensures that the neuron responds to a single body region, while the other latent inputs are suppressed. When the body part containing the receptive field of a given neuron is deleted, this inhibitory process becomes imbalanced, and these latent connections are unmasked. Thus, neurons that represented a finger become responsive to stimulation of adjacent body parts, such as the other fingers and palm, within minutes of finger amputation (Merzenich et al., 1984).

Such experiments have clear implications for body mereology, because they show that the differentiation of the whole body into constituent parts reflects a dynamic process of neural competition between representations in the somatosensory system. Differentiation of body parts may be partly innately encoded. Indeed, aplasic patients born with a limb missing still feel the presence of a phantom body part (see Brugger, this volume), implying

an innate structured body representation. Interestingly, the phenomenon of phantom limb can be understood only if we take into account the body as a whole. Indeed, we cannot explain the existence of the phantom limb if we consider it independently from others parts of the body: where can it come from, as there is no sensory information from the absent limb? However, the change induced by amputation is not only local, since the neural representation of other regions of the body reorganizes to invade the relevant area of cortex. Body parts should thus not be understood in isolation, but always on the background of their relationship with other body parts.

While phantom limbs results from the physical deletion of body parts, personal neglect reflects the mental deletion of body parts. Patients forget the existence of one side of their body or even deny the ownership of one of their limbs. Indeed, somatosensory information does not automatically suffice for feeling a sense of ownership toward the body that I directly perceive. For instance, Bottini et al. (2002) reported the case of F.B, an asomatognosic patient who was unable to report touches delivered on her left hand and who attributed it to her niece. The examiner slightly touched one of her hands and warned F.B. that he was going to touch (a) her right hand, (b) her left hand, (c) her niece's hand. The examiner asked her to report whether she felt a tactile sensation while she was blindfolded. The results showed that she was unable to report any tactile sensation on her "alien" hand in condition (b), but that her tactile anesthesia completely recovered in condition (c). In other words, she could feel the touch only on her so-called "niece's hand". Consequently, the mental boundaries of one's own body are not only fixed by proprioceptive inputs, but result rather from more complex phenomena, that we will investigate in the second part.

<u>Addition</u>

What would happen to the neural and psychological representation of the body if a body part were added rather than removed? This question at first seems silly. Although body parts change considerably in size and slightly in shape with normal lifespan development and disease, their number, differentiation and identity do not normally change. However, experimental neuroscience, neurology and neuropsychiatry all suggest that the brain's mereology of the body is sufficiently plastic to incorporate and subsume new body parts. Here, we briefly review addition of body elements in somatoparaphrenic delusions involving supernumerary limbs, in tool use and in anosognosia.

The neurological phenomenon of "supernumerary limb" can be interpreted in terms of failure to inhibit a mechanism that maintains body space. In one form of this rare condition, the patient reports the presence of an additional arm. The supernumerary arm typically has the correct anatomical parts, though its size may be unusual and change over time. Interestingly, the arm is often experienced as attached to the body at the midline (Boisson & Luaute, 2004). Hari et al. (1998) described a patient with frontal and callosal lesions who experienced ghost supernumerary limbs in the location previously occupied by the left arm or leg. Subsequent fMRI comparisons between periods when the additional limb was and was not experienced showed an increased activity in the supplementary motor area during the delusion (McGonigle et al., 2002). The authors speculated that the delusion arose because the lesion had produced a fractionation between the normally coherent efferent and afferent representations of the body. As a result, the efferent and afferent signals gave rise

to two separate bodily percepts, rather than a single integrated whole. These results suggest that a specific neural mechanism maintains a coherent representation of body parts by integrating several sensory and motor inputs. In the next section of this paper, we describe studies of the Rubber Hand Illusion in normal subjects which seem to rely on a similar mechanism.

Tool use is a characteristic feature of many animals, and is often taken as a hallmark of intelligence. Several recent studies suggest that neural representations of the body may be altered when using a tool to extend the subject's reaching space (see Maravita and Iriki, 2004; Maravita, this volume). Studies of bimodal neurons in monkey parietal cortex have focused on the spatial relation between visual and tactile receptive fields. Tactile receptive fields on the hand gradually displaced of their visual receptive field from an initial position near the hand towards the tip of the tool, as a function of tool learning (Iriki et al. 1996). In human subjects with unilateral lesions, active use of a tool improved the cross-modal links between visual stimuli at the tool tip and tactile events at the hand (Maravita et al. 2002; Farne and Ladavas, 2000). Mereologically, the tool appears to become a new segment of the limb within the cognitive body representation. Alternatively, the tool may become incorporated into the representation of an existing segment, with an appropriate adjustment to segment length. These neural changes may underlie the anecdotal observation that a person using a tool experiences tactile sensations located at the tool tip.

A recent neuropsychological study reinforces the idea of a specific brain process associated with addition of elements to body representations. Aglioti et al. (1996) reported the case of a patient who denied ownership of her left hand following a right-hemisphere lesion. She likewise denied ownership of a ring worn on her left hand. When the same ring was worn on the unaffected right hand, she correctly recognized it as belonging to her. The ring attached to the body was processed in the same way as the hand to which it was attached by the brain processes responsible for creating a coherent sense of the body. That is, the ring was incorporated into the mental representation of the hand on which it was worn. These data suggest that body representations are flexible and can dynamically include new components under proper conditions that we will investigate in the next section. Such cases also demonstrate an intriguing link between sensorimotor representation of body parts and the sense of self, which has been discussed elsewhere (Haggard et al., 2003).

In summary, the mental map of the body is characterized both by its internal organization and by its borders. Body mereology addresses two main questions: (1) how do we differentiate the body into parts (segmenting process)? (2) how are the body parts organized (structuring process)? The reply varies according to the somatosensory mereology and the motor mereology.

INSERT TABLE 1 AROUND HERE

2. Multisensory body mereology

Phenomena of addition and deletion of body parts would remain a mystery if we describe the brain as a passive receptor of sensory information. Body representations do not merely reflect peripheral inputs, but are the result of an active process of integration of

afferent information (vision, proprioception, and touch) and efferent signals. The consistency between several sources of information provides a strong cue for individuating body parts. More particularly, visual information plays an important role in the addition of body parts. Indeed, somatosensory perception is often quite local and provides little information about the relation between body parts, while vision carries global information about the body as a whole and has the capacity to link together the different body parts. Multisensory integration can thus provide a window into the investigation of bodily synthesis.

In this section, we use a specific example of multisensory integration, the so-called "Rubber Hand Illusion" to illustrate how the mind constructs a synthesis of the body as a whole using sensory inputs from specific body parts. This section therefore emphasizes the importance of the holistic component of body representation in the integration of body parts. This corresponds to the key mereological question of how the whole relates to the sum of the parts. We will suggest that body parts are individuated on the basis of multisensory matching. Furthermore, we will distinguish two kinds of mechanisms involved in self-attribution of body parts: a bottom-up process based on Bayesian correlation and a top-down process based on the synthetic representation of the body as a whole.

2.1 The body as a "common sensible"

The body space is what Aristotle called a "common sensible", i.e., a property represented by different modalities. The multisensory nature of the body has usually been neglected by the philosophical tradition, which has focused more on contrasting the body with other physical objects, or bodies of other people (Merleau-Ponty, 1945; Anscombe, 1959). The multisensory nature of the body has been considered only to emphasize the private inner knowledge that we have for our own body. Internal perception such as nociception and proprioception may even be considered as the primitive core of self-consciousness (Bermudez, 1998). However, this approach ignores the fact that our knowledge of our bodies typically results from the integration of plurimodal information.

Several studies show the importance of the interaction between vision, touch and proprioception (Driver and Spence, 1998). Indeed, visual information alters tactile sensation and tactile stimulation orients visual attention. The sight of body parts increases temporal and spatial tactile sensitivity: visual information about your hand can reduce tactile target detection time and improve tactile spatial resolution (Kennett et al., 2002). The cross-modal effect can be so strong that vision of the hand being touched may elicit a tactile sensation, even if no real touch occurs (Halligan et al., 1997).

These cross-modal effects may rely on two kinds of neural mechanisms. Electrophysiological studies in the monkey have shown in the premotor and the parietal cortex the existence of bimodal neurons that combine visual and somesthetic signals (Duhamel et al., 1997; Graziano, Cooke et Taylor, 2000). Furthermore, recent experiments suggest that back-projections from multimodal areas to unimodal areas may also play a role (Macaluso, Frith and Driver, 2000; Taylor-Clarke, Kennett and Haggard, 2002). In brief, heteromodal areas integrate the different sources of information, but the perceptual consequences of these interactions could be also realized in the so-called unimodal areas

(Calvert et al., 1998). Thus, primary areas may be unimodal in terms of their afferent information, yet they may be affected by other kinds of signals.

Therefore, despite the fact that all sensory modalities do not always provide the same representation of the body, we tend to maintain consistency by the resolution of sensory conflicts and we experience a single unified body representation. How is such integration possible? The main problem is to understand how the relevant elements to bind as a single entity are selected and segregated (Treisman, 1998). In other words, how do I avoid combining together proprioceptive information from my own hand and visual information from your hand or even from the table? According to Ramachandran, there is no active binding process. Mere conjunction between sensory inputs is sufficient to integrate any object within the body. However, we will argue from the high consistency of body representations that this is not the case.

In order to be integrated, the different kinds of information have to be considered as being from a common source. Then the question is to understand how this source is individuated. We may draw a parallel with selective attention: what is the nature of the underlying units of attention? Traditional models such as Posner's one characterize attention in spatial terms: we code one stimulus at a time selected on the basis of its location and excluding stimuli from other locations. In contrast, recent models emphasize the role of discrete objects: we attend to independent individuals that we can track over the time, rather than to spatial regions of the visual field (Scholl, 2001). If we apply the distinction between space-based and object-based attention to the problem of multimodal body representations, we may sketch two hypotheses. According to the first one, it is sufficient to assign a common spatio-temporal source to somesthetic and visual information (Armel and Ramachandran, 2003). We will defend instead a second hypothesis that a cognitive body representation modulates the integration of visual and somesthetic information.

2.2 Self-attribution of a rubber hand

The Rubber Hand Illusion (RHI), originally reported by Botvinick and Cohen (1998), can serve as an experimental paradigm, which can address the relationship between multisensory mereology and the body. This claim is supported by the fact that the constituting elements of the illusion involve visual and tactile events, and the integration of these percepts produces strong phenomenological and behavioral responses that are bodily-related.

In the original experiment (Botvinick & Cohen, 1998), subjects sat with their left arm resting on a table, hidden behind a screen. They were asked to fixate at a rubber hand presented in front of them, and the experimenter stroked with two paintbrushes both the subject's hand and the fake hand simultaneously. After the stimulation period, subjects reported that:

a.   They felt as if the rubber hand were their own hand.

b.   It was as if subjects were feeling the touch of the paintbrush in the location where they saw the rubber hand touched.

c.   They *did not* feel as if their (real) hand were drifting towards the rubber hand.

Surprisingly, and contrary to the introspective evidence (see point (c) above), when subjects were asked to indicate the felt position of their own hand after the stimulation period, they perceived their hand to be closer to the rubber hand than it really was. That was true only when the two hands were synchronously stimulated, and not when both hands were asynchronously stimulated. According to Botvinick and Cohen, "the effect reveals a three-way interaction between vision, touch and proprioception, and may supply evidence concerning the basis of bodily self-identification" (Botvinick & Cohen, 1998, p.756). In other words, vision captured the tactile sensations, and this inter-sensory match led to proprioceptive alteration. This result seems to suggest that "intermodal matching can be sufficient for *self-attribution*" (italics added, p.756). This conclusion can be justified by the fact that proprioception is generally thought to be the sense of the self *par excellence* (Bermudez, 1998).

Armel and Ramachandran (2003) stimulated the subjects' hand and a rubber hand synchronously or asynchronously. After the stimulation, they "injured" the fake hand and measured skin-conductance responses (SCRs) from the subjects' unstimulated hand. SCRs were stronger after synchronous stimulation compared to asynchronous stimulation between the real and fake hands. Even more surprisingly, differences between synchronous and asynchronous conditions were also significant when subjects were looking, not at a fake hand, but at the table being stroked. The authors concluded that this illusion ("it feels like the fake hand/table is my hand", p.1504) is the result of Bayesian perceptual learning, and they observed that "the brain's remarkable capacity for extracting statistical correlations in sensory input is most apparent in the table condition" (p.1505). That would suggest that the RHI is simply the result of an association between synchronous visuo-tactile events, a purely bottom-up mechanism, and that *any* object can become part of *me*, simply because strong statistical correlations between different sensory modalities are both necessary and sufficient conditions for "deceiving our brains".

On this view, psychological concepts such as embodiment and selfhood are unnecessary, because purely Bayesian principles of statistical correlation are sufficient to extend the body representation, to include even "body parts" as implausible as tables (Armel & Ramachandran, 2003). Another hypothesis derived from this Bayesian account of the RHI is that proprioceptive drifts should be significant larger only for the stimulated body-part, and smaller or even absent for unstimulated body-parts. We tested this hypothesis in two experiments, in which contrary to the experiment by Botvinick and Cohen, we stimulated only one (experiment 1) or two (experiment 2) fingers, and not the whole hand (Tsakiris & Haggard, under revision).

In experiment 1, subjects viewed a rubber hand being stroked by a paintbrush on either the index or the little finger. The subject was always stroked by a similar paintbrush on the same finger as the rubber hand was stroked. However, the rubber hand and the subject's hand were stroked either synchronously in the experimental condition, or asynchronously in the control condition. We obtained judgments for the felt position of the index finger or for the little finger in different blocks. Participants judged the felt position of their finger(s) by indicating a number on a ruler that was presented in front of them and at the same gaze depth as the rubber hand. During judgment, both the rubber hand and the participant's hand were out of view. We used the proprioceptive drift as a convenient, continuous and quantitative measure of self-attribution. Proprioception is intimately related to sense of

bodily self (Bermudez, 1998), but it is not a direct measure of self-attribution *per se*. The results showed that only the stimulated finger was perceived to be significantly drifted towards the rubber hand (see Figure 3a).

INSERT FIGURE 3 AROUND HERE

This effect was further replicated in experiment 2, in which both the index and the little fingers were stimulated across all conditions, but the pattern of stimulation was manipulated independently on each finger. This manipulation guaranteed that each finger received equal amount of stimulation in each condition. Our first analysis focused on the differences in the perceived position of index *vs.* little finger, in the condition where "index was stroked synchronously/little asynchronously" compared to the condition where "little finger was stroked synchronously/index asynchronously". The analysis replicated the finding of the previous experiment, because only the finger that was synchronously stimulated was perceived to be significantly closer to the rubber hand (see Figure 3b), suggesting that synchronous visual and tactile correlation is a necessary condition for the built-up of the illusion. These data confirm the Bayesian hypothesis because the proprioceptive drifts were localized to the stimulated finger(s).

However, as part of experiment 2, we also stimulated both the index and the little fingers synchronously or both asynchronously with respect to the rubber fingers, and obtained judgments for the felt position of the middle finger, which was never stimulated. By comparing the perceived position of the middle finger when both the little and index fingers were stimulated asynchronously to the condition when both fingers were stimulated synchronously, we showed that synchronous stimulation caused the unstimulated middle finger to drift just as much as the little and index fingers which were stimulated. This finding suggests that there is a spreading gradient of the RHI to unstimulated fingers. Therefore, the localized proprioceptive drift is not absolute. A cognitive, mereological representation of the arrangements of fingers may explain the observed spreading of the effect to the unstimulated middle finger. A purely Bayesian account can not explain why the middle finger drifted at all in the absence of any stimulation. If the RHI can extend to body parts that are not stimulated, is it also possible to have synchronous stimulation without inducing the RHI? If so, local multisensory integration would then be neither necessary nor sufficient for bodily synthesis.

The finding of a RHI effect for an unstimulated finger suggests that factors other than local multisensory integration may be sufficient for self-attribution. We suggest that coherence with a cognitive body representation may be one such factor. To test this hypothesis we manipulated the felt and seen hand identities. In experiment 3, we stimulated the middle finger of the subject's left hand, while they were looking at a left or a right rubber hand being stimulated on the middle finger. As shown in Figure 4a, we found large proprioceptive drifts when subjects were looking at a congruent rubber hand identity and almost no drifts when they were looking at the middle finger of an incongruent rubber hand identity. The fact that we observed a negative effect (i.e. no drift) in the presence of stimulation suggests that mere statistical correlation between visual and tactile events is not sufficient for the inducement of the RHI, as measured by proprioceptive drift. These data suggest that the need for compatibility between the felt and seen sensation goes beyond the level of spatial and temporal congruency. We suggest that body representations play a modulatory top-down role in this process of body-related multisensory integration.

In experiment 4, we further investigated the role of such body representations. First we asked whether the RHI would occur if the rubber hand was in an incongruent posture (e.g. rotated by -90°) with respect to the subject's own hand. Second, we asked whether a neutral object (e.g. a wooden stick) would induce similar effects. The results showed that the subjects mislocalized the position of their own hand *only* when the rubber hand was in congruent posture (see Figure 2b). In other words, synchronous stimulation between the subject's hand and a rubber hand at an incongruent posture or a neutral object did not elicit the RHI, at least as it is measured by proprioceptive drifts. These findings imply that mere correlation between visual and tactile percepts is not a *sufficient* condition for self-attribution of a rubber hand or any other object, at least not when the subject's body-configuration is not respected.

Overall, the results obtained in these experiments argue against a purely Bayesian interpretation of the relationship between intermodal matching and self-attribution. First, a neutral object did not elicit any significant difference in the perceived position of the subjects' hand. Even when this neutral object was replaced by a rubber hand, the synchronicity of visual and tactile events did not suffice for the inducement of the RHI, because of the incongruence between the rubber hand and the subjects' own hand at a level that goes beyond synchronous stimulation. Hand posture and hand identity have been identified as two kinds of body space influence that modulate the visuo-tactile integration underlying the RHI (see also Pavani, Spence & Driver, 2000, and Rorden et al., 1999). Graziano and colleagues made similar observations during the recording of bimodal neurons in parietal area 5 (Graziano, Cooke, Taylor, 2000). These bimodal neurons of the monkey brain were sensitive to the position of the fake arm when fake and real hands were stroked synchronously, but *only* when the fake arm was aligned with the monkey's body. Such findings provide support for an active role of body representations in the processes underlying the RHI. It seems that attribution requires a plausible and congruent visual object to bind with a body part, with respect to the general body space configuration.

At first sight, the localized effects in experiments 1 and 2 provide support for the Bayesian approach, because stronger statistical correlations are expected for the stimulated finger(s). Nevertheless, two of our findings challenge a strict Bayesian account. First, the unstimulated middle finger drifted to an equivalent extent when two fingers were stimulated synchronously (experiment 2). The experience of ownership of the rubber hand is global. In other words, participants did not feel as if only the stimulated finger was their own finger, but they felt as if the whole rubber hand was part of them. Second, a synchronously stimulated middle finger did not drift when subjects were looking at an incongruent rubber hand identity (experiment 3). A purely bottom-up account cannot explain either of these effects.

However, the RHI is a purely passive experience, and to that extent it lacks ecological validity. Intermodal matching in real life occurs within a dynamic and active interaction between the agent and the environment, during which multimodal sensory and also motor signals need to be integrated, but also differentiated on the basis of their origin. A recent experiment on self-recognition shows that efferent information clearly contributes to the ability to match proprioceptive and visual representations of a remote bodily effect (Tsakiris & Haggard, under revision). Subjects experienced a passive extension of the right

index finger, either as an effect of a movement of their own left hand ('self-generated action'), or imposed externally by the experimenter ('externally-generated action'). The visual feedback was manipulated so that subjects could see either their own right hand ('view own hand' condition) or someone else's right hand ('view other's hand condition) undergoing an equivalent passive extension of the index finger. Self-recognition was significantly more accurate when the passive displacement of the right hand was self-generated, even though there was congruent visuo-proprioceptive feedback across conditions, and despite the fact that it was the affected right hand and not the acting left hand that the subjects were watching. In the absence of efferent information, congruent visual and proprioceptive feedback, as is the case in the RHI, led to a misattribution of the moving hand.

Taken overall, such results favor an interplay between bottom-up and top-down influences in the process of bodily synthesis. Even though intermodal matching seems to be a pre-requisite for self-identification and self-attribution, the RHI suggests that our sense of our body is more than the sum of the correlated visual and tactile percepts. Therefore, multi-sensory percepts are not integrated in a simple additive manner, but instead respect a set of conditions that guarantee the functional and phenomenological coherence of the experienced body. This set of background conditions constitutes a cognitive model or representation of the body and its part relations. The involvement of this model may explain the specific and vivid phenomenology that characterizes multisensory integration of bodily information in the RHI.

Conclusion: The body and the self

Mereology raises the following questions: how do I differentiate the parts of the body? what is the relationship between the hand and the body? how do I know that the hand belongs to the body? We have investigated the principles of body mereology governing segmenting, structuring and grouping. From a phenomenological point of view, bodily experiences display a unity and a consistency that have to be explained in the context of the body as an integrated agent in interaction with the world.

The mereology of the sensing body begins with an undifferentiated somatosensory sheet. Here, relationships between the body parts are based on spatial contiguity in a cortical map. The body parts do not seem to be explicitly differentiated in a categorical way. Body part *categories* seem to arise only at a higher, cognitive level of representation. In several cases, vision of body parts may play an important role in providing this structure. Finally, the geometric mereology of the body has been studied by judgments of body part size. These studies suggest that the spatial arrangement of body parts is a fusion or interpretation of available multi-sensory information from across the whole body. The phenomena of phantom limb and supernumerary limbs illustrate the plasticity of the sensing body as well as the relationship between the body parts: what one feels in one body part may depend on what one feels in another.

In contrast, voluntary action seems to presuppose a perfectly segmented and consistent representation of the body. If I decide to lift my arm, I must be able to distinguish my arm from other body parts. Action thus plays a dual role. First, it structures or segments the mental representation of the body into functional units of movements defined by the joints.

Second, action groups disparate body parts together, for example when all my fingers work together to grasp a glass in a coordinated grip. We suggest that phenomenal experience of the acting body therefore represents body parts in a more global way than experiences of the sensory body. Consequently, the mereology of the sensing body and the mereology of the acting body provide different ways of differentiating and grouping body parts. Efferent mereology may be more consistent than afferent mereology. However, in both cases, body parts are not represented in isolation, but are interpreted in their interaction with other body parts as well as with the body as a whole.

We have thus suggested that somatosensory mereology is based on spatial contiguity, while motor mereology is based on functional coherence of body movements during intentional actions. In contrast, it seems that multisensory mereology is intimately related to the sense of ownership of body parts. Indeed, body parts are experienced not only as parts of the body, but also as parts of *one's own* body. Therefore, we may ask how one self-attributes body parts. More particularly, is the sense of ownership the cause or the result of the multisensory synthesis of bodily information? We think that this is a modern neuroscientific instance of the old contrast between Humean and Kantian views of the self. According to Hume, we are confronted with a "bundle" of bodily experiences. The sense of ownership results from their synthesis into a consistent representation of the body as a whole. The results of Botvinick and Cohen (1998) and Armel and Ramachandran (2003) agree with this view. These authors argue that intermodal matching is sufficient condition for the sense of ownership. Developmental psychology also suggests that multimodal integration is at the source of the recognition of one's own body (Rochat, 1998). However, we have presented data from the Rubber Hand Illusion suggesting that it is not in fact sufficient. We do not self-attribute a piece of wood or the contralateral hand, at least on the basis of the quantitative measures used in our study. Furthermore, if the embodied self is merely the result of bodily synthesis, what role does it play? It would be purely epiphenomenal.

In contrast, according to the Kantian hypothesis, self-attribution is a prerequisite of multimodal integration: I self-attribute bodily experiences ("I see my hand" and "I feel my hand") *before* combining them into a unified experience of the multisensory body. I thus avoid mistakenly combining the tactile perception of my hand with the visual experience of someone else's hand. Self-consciousness would thus constitute a prior necessary condition of body synthesis. On this view, the RHI should never occur at all, since I know that the rubber hand is not part of me. Therefore, I should be unable to include it in an integrated multisensory bodily experience. More importantly, the Kantian view leaves open the source of self-consciousness: if the embodied self does not result from the multisensory integration of bodily information, where does it come from? We suggest that neither of these classical theories of the self is consistent with modern neuroscientific and psychophysical data on bodily sensation. Consequently, we would like to suggest a third hypothesis: the sense of ownership arises from the integration of afferent, and also efferent sources of information. However, this integration process is also modulated by a synthetic cognitive model of the body as a whole.

References

Aglioti, S., Smania, N., Manfredi, M., Berlucchi, G. (1996), Disownership of left hand and objects related to it in a patient with right brain damage. *NeuroReport*, 8, 293-296.

Anscombe, G.E.M. (1959), *Intention*. Oxford: Blackwell.

Armel K.C, Ramachandran V.S. (2003), Projecting sensations to external objects: evidence from skin conductance response. *Proc R Soc Lond B Biol Sci*, 270(1523), 1499-506.

Bermudez, J.L. (1998), *The Paradox of Self-Consciousness*. Cambridge (Mass.): MIT Press.

Blankenburg, F., Ruben, J., Meyer, R., Schwiemann, J., Villringer, A. (2003), Evidence for a rostral-to-caudal somatotopic organization in human primary somatosensory cortex with mirror-reversal in areas 3b and 1. *Cereb Cortex*, 13(9), 987-93.

Block, N. (1983), Mental pictures and cognitive science. *Philosophical Review*, 92, 499-541.

Boisson, D. and Luaute, J. (2004), Les somatoparaphrénies. *Annales Médico Psychologiques*, 162, 55-59.

Bottini, G., Bisiach, E., Sterzi, R., Vallar, G. (2002), 'Feeling touches in someone else's hand', *Neuroreport*, 13, 249-252.

Botvinick, M., Cohen, J. (1998), Rubber hands 'feel' touch that eyes see. *Nature*, 391, 756.

Braun, C., Schweizer, R., Elbert, T., Birbaumer, N., Taub, E. (2000), Differential activation in somatosensory cortex for different discrimination tasks. *J Neurosci*, 20(1), 446-50.

Calvert, G.A., Brammer, M.J., Iversen, S.D. (1998), Crossmodal identification. *Trends in Cognitive Sciences*, 2 (7), 247-253.

Castiello, U., Paulignan, Y., & Jeannerod, M. (1991). Temporal dissociation of motor responses and subjective awareness. A study in normal subjects. Brain, 114, 2639–2655.

Driver, J. and Spence, C. (1998), Attention and the cross-modal construction of space. *Trends in Cognitive Sciences*, 2(7), 254-262.

Duhamel, J.R., Bremmer, F., BenHamed, S., Graf, W. (1997), Spatial invariance of visual receptive fields in parietal cortex neurons. *Nature*, 389(6653), 845-848.

Farne, A., Ladavas, E. (2000), Dynamic size-change of hand peripersonal space following tool use. *Neuroreport*, 11(8), 1645-9.

Fourneret, P. and Jeannerod, M. (1998), Limited conscious monitoring of motor performance in normal subjects. *Neuropsychologia*, 36 (11), 1133-1140.

Gandevia, S.C., Phegan, C.M. (1999), Perceptual distortions of the human body image produced by local anaesthesia, pain and cutaneous stimulation. *J Physiol*, 514, 609-16.

Graziano, M.S., Cooke, D.F., Taylor, C.S. (2000), Coding the location of the arm by sight. *Science*, 290(5497), 1782-6.

Gurwitsch, A. (1985), *Marginal consciousness*. Athens: Ohio University Press.

Haggard P, Taylor-Clarke M, Kennett S. (2003), Tactile perception, cortical representation and the bodily self. *Current Biology*, 13(5), R170-3.

Halligan, P.W., Marshall, J.C., Hunt, M., Wade, D.T. (1997), Somatosensory assessment: can seeing produce feeling? *J Neurol*, 244(3), 199-203.

Hari, R., Hanninen, R., Makinen, T., Jousmaki, V., Forss, N., Seppa, M., Salonen, O. (1998), Three hands: fragmentation of human bodily awareness. *Neurosci Lett*, 240(3), 131-4.

Hlustik, P., Solodkin, A., Gullapalli, R.P., Noll, D.C., Small, S.L. (2001), Somatotopy in human primary motor and somatosensory hand representations revisited. *Cereb Cortex*, 11(4), 312-21.

Iriki, A., Tanaka, M., Iwamura, Y. (1996), Coding of modified body schema during tool use by macaque postcentral neurones. *Neuroreport*, 7(14), 2325-30.

James, W. (1890), *The principles of Psychology*, Vol 1. New York: Holt.

Jeannerod, M. (1997), *The Cognitive Neuroscience of action*. Oxford: Blackwell.

Kennett, S., Spence, C., Driver, J. (2002), Visuo-tactile links in covert exogenous spatial attention remap across changes in unseen hand posture. *Percept Psychophys*, 64(7), 1083-94.

Kinsbourne M., Warrington E. (1962), A study of finger agnosia. *Brain*, 85, 47-66.

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

Lemon, R. (1988), The output map of the primate motor cortex. *Trends in Neuroscience*, 11 (11), 501-506.

Macaluso, E., Frith, C., Driver, J. (2000), Selective spatial attention in vision and touch: unimodal and multimodal mechanisms revealed by PET. *J Neurophysiol*, 83(5), 3062-75.

Maravita, A. and Iriki, A. (2004), Tools for the body (schema), *Trends in Cognitive Sciences,* 8 (2), 79-86.

Maravita, A., Clarke, K., Husain, M., Driver, J. (2002), Active tool use with the contralesional hand can reduce cross-modal extinction of touch on that hand. *Neurocase*, 8(6), 411-6.

McGonigle, D.J., Hanninen, R., Salenius, S., Hari, R., Frackowiak, R.S., Frith, C.D. (2002), Whose arm is it anyway? An fMRI case study of supernumerary phantom limb. *Brain*, 125, 1265-74.

Merleau-Ponty, M. (1945), *Phénoménologie de la perception*. Paris: Gallimard.

Merzenich, M.M., Nelson, R.J., Stryker, M.P., Cynader, M.S., Schoppmann, A. and Zook, J.M. (1984), Somatosensory cortical map changes following digit amputation in adult monkeys. *J. Comp. Neurol.* 224, 591–605.

Ogden, J.A. (1985), Autotopagnosia. Occurrence in a patient without nominal aphasia and with an intact ability to point to parts of animals and objects. *Brain*, 108, 1009-22.

O'Shaughnessy, B. (1980), *The will: dual aspect theory*. Cambridge: Cambridge University Press.

O'Shaughnessy, B. (1995), Proprioception and the body image. In *The body and the self*, edited by J.L. Bermudez, A. Marcel and N. Eilan, Cambridge (Mass.): MIT Press.

Pavani F, Spence C, Driver J. (2000), Visual capture of touch: out-of-the-body experiences with rubber gloves. *Psychological Science, 11*(5):353-9.

Penfield, W., Boldrey, E. (1937), Somatic motor and sensory representation in the cerebral cortex of man as studied by electrical stimulation. *Brain*, 60, 339-448.

Penfield, W., Rasmussen, T. (1950), *The Cerebral Cortex of Man.* New York: MacMillan.

Ramachandran, V.S., Rogers-Ramachandran, D. (1996), Synaesthesia in phantom limbs induced with mirrors. *Proceedings of the Royal Society of London*, 263, 377-386.

Ramachandran, V.S., Hirstein, W. (1998), The perception of phantom limbs. *Brain*, 121, 1603-1630.

Reed C.L., Stone V.E., Bozova S., Tanaka J. (2003), The body-inversion effect. *Psychol Sci*, 14(4), 302-8.

Rochat, P. (1998), Self perception and action in infancy. *Experimental Brain Research*, 123, 102-109.

Rorden C, Heutink J, Greenfield E, Robertson IH. (1999), When a rubber hand 'feels' what the real hand cannot. *Neuroreport, 10*(1):135-8.

Schieber, M.H., Hibbard, L.S. (1993), How somatotopic is the motor cortex hand area? *Science*, 261(5120), 489-92.

Scholl, B.J. (2001), Objects and attention : the state of the art. *Cognition*, 80 (1-2), 1-46.

Schweizer, R., Braun, C., Fromm, C., Wilms, A., Birbaumer, N. (2001), The distribution of mislocalizations across fingers demonstrates training-induced neuroplastic changes in somatosensory cortex. *Exp Brain Res*, 139(4), 435-42.

Semenza, C. (1988), Impairment in localization of body parts following brain damage. *Cortex*, 24(3), 443-9.

Sirigu, A., Grafman, J., Bressler, K., Sunderland, T. (1991), Multiple representations contribute to body knowledge processing. Evidence from a case of autotopagnosia. *Brain*, 114, 629-42.

Taylor-Clarke, M., Kennett, S., Haggard, P. (2002), Vision modulates somatosensory cortical processing. *Curr Biol*, 12(3), 233-6.

Taylor-Clarke, M., Jacobsen, P., Haggard, P. (2004), Keeping the world a constant size: object constancy in human touch. *Nat Neurosci*., 7(3), 219-20.

Treisman, A. (1998), Feature binding, attention and object perception. *Philos Trans R Soc Lond B Biol Sci*, 353(1373), 1295-306.

Tsakiris, M., Haggard, P., Franck, N., Mainy, N., Sirigu, A. (2004). A specific role for efferent information in a self-recognition task. *Cognition*, under revision.

Tsakiris, M. and Haggard, P. (2004). Of rubber hands and rubber fingers. *Journal of Experimental Psychology : Human Perception and Performance*, under revision.

Wiggins, D. (1968), On being in the same place at the same time. *The philosophical review*, 77 (1), 90-95.

Wiggins, D. (1980), *Sameness and Substance*. Oxford: Blackwell.

	Somatosensory mereology	Motor mereology
Physical origin	Skin	Muscle and joints
Primary cortical area	SI	MI
Internal structure	Continuous somatotopy	Integrated and overlapping somatotopy
Segmenting principle	No intrinsic segmentation	Action
Landmarks for body segmentation	None	Joints
Structuring principle	Contiguity	Coherence
Organization	Spatial	Functional
Confusion of body parts	Autotopagnosia	Motor neglect
Addition of body parts	Supernumerary limbs	Tool use
Deletion of body parts	Phantom sensations	Phantom movements

Table 1.

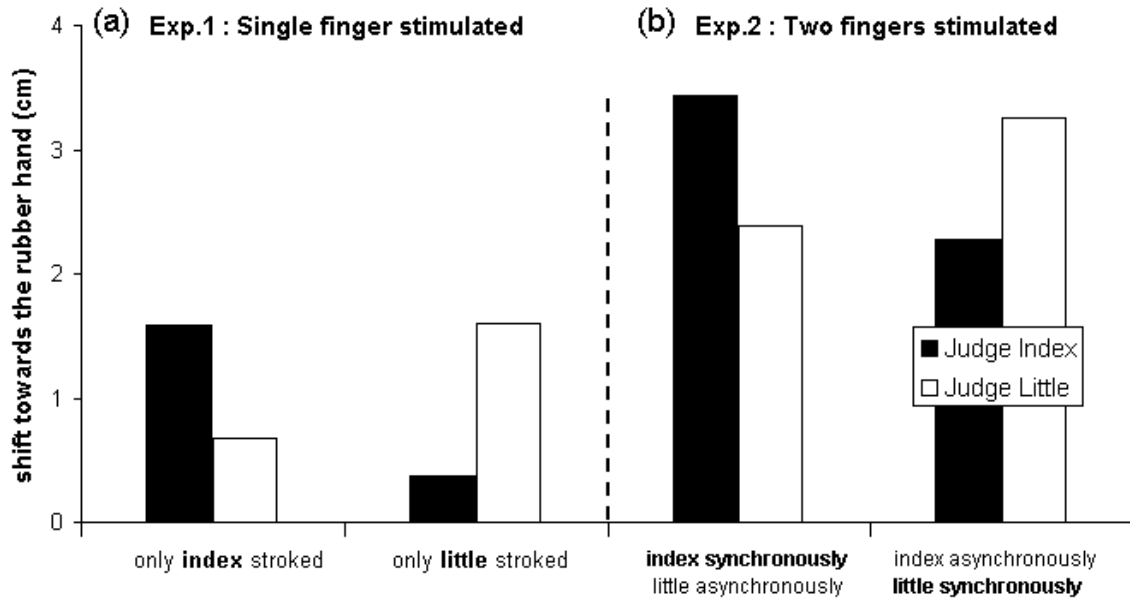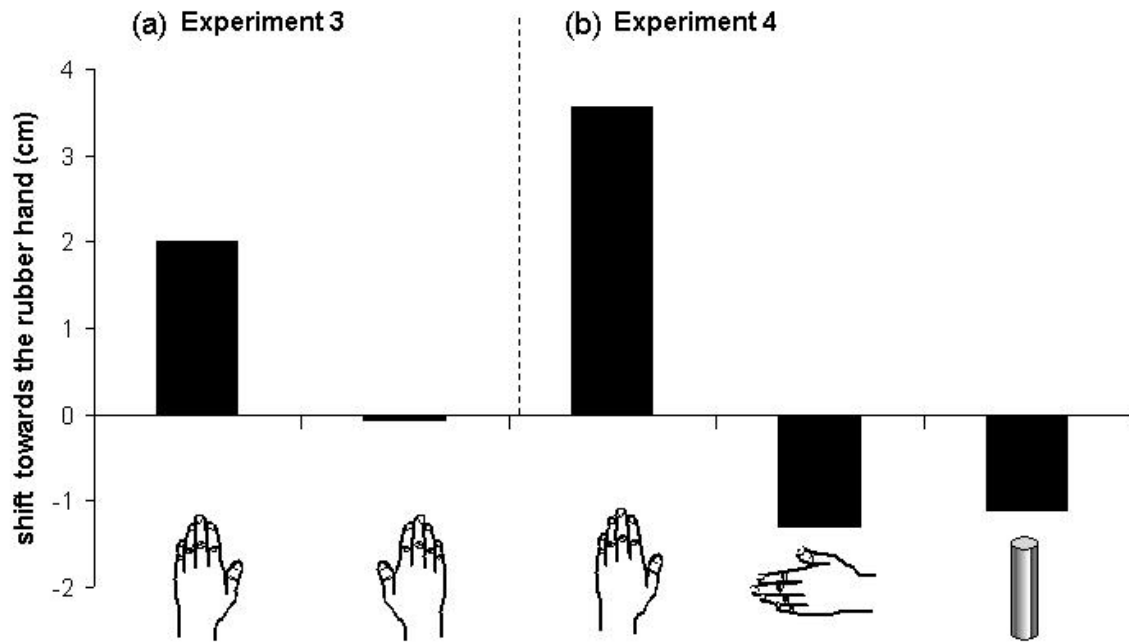**Figure 1**

Figure 2

Figure 3

Figure 4

Figure Legends

Table 1: Somatosensory and motor mereology

Figure 1: Body representation in (a) human motor cortex and (b) human somatosensory cortex. (Adapted from Penfield and Rasmussen, 1950)

Figure 2: The Pinocchio illusion. Experimental configurations and results with (A) biceps brachii vibration and (B) triceps brachii vibration. From Lackner (1998)

Figure 3: Mean perceptual shifts across conditions for experiments 1 and 2. To isolate the part of the positional drift due to visual-tactile integration, and obtain a true measure of RHI, we subtracted the judgment errors obtained in the asynchronous conditions from the judgment errors obtained in the synchronous conditions.

Figure 4: Mean perceptual shifts across conditions for experiments 3 and 4. In experiment 3, subjects judged the perceived position of the stimulated middle finger. In experiment 4, subjects judged the perceived position of the stimulated index finger.