

Dynamic spatial cognition: Components, functions, and modifiability of body schema¹

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Abstract: There has been substantial progress towards the understanding of the classical notion of “body schema,” with recent advances in experimental methodology and techniques. Mental rotation of the hands can be used as a tool to investigate body schema. Research has shown that implicit motor imagery (i.e., mental simulated movements) can be generated based on the body schema, by combining both stored and incoming sensory information. Multimodal stimulation of peripersonal space has also served as an experimental paradigm for the study of body schema. Perception of peripersonal space is based on body-part-centered space coding that is considered as a manifestation of the body schema, its function being to integrate visual, tactile, and proprioceptive information, and perhaps motor plans as well. By combining such experimental paradigms with neuroimaging and neurophysiological techniques, research has converged to show that the parietal association cortex and premotor cortex are important for the body schema. Multimodal perception of body parts and peripersonal space have been also studied in relation to prism adaptation and tool use effects, indicating a clear modifiability of the body schema. Following prolonged adaptation to reversed vision, a reversed hand representation can be added to the body schema like a tool. The stored component of the body schema may not be established well in young children. But once established it may not be deleted even after an arm is amputated, although it may be weakened. All of these findings help to specify properties of the body schema, its components, functions, and modifiabilities.

Key words: body schema, motor imagery, peripersonal space, body-part-centered coordinates, phantom limb.

To achieve appropriate goal-directed movements in space, we need to process incoming information about the spatial location of nearby objects and that of our own body parts. In addition, we must link visual, proprioceptive, and motor signals. Such linkage presumably depends on some internal representation of the body, such as the classical notion of body schema (Head, 1918), which has been assumed as a functional element for perceiving one's own body in environmental space. Although little is known about the neuronal mechanism,

recent advances in neuroscience and psychology have come close to capturing various aspects of body schema. A growing body of evidence shows that hands and arms are sources for the integration of incoming and stored multimodal information, including visual, proprioceptive, and motor signals. This article reviews several lines of recent psychological and neuroscientific findings relevant to exploring “body schema”, which is supposed to serve for space recognition and motor control. Hands and arms were focused on in the present study.

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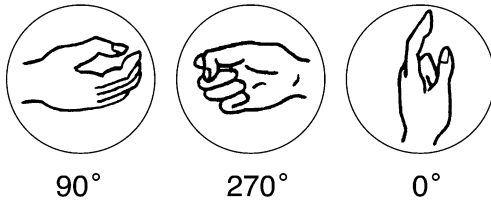


Figure 1. Examples of stimuli in the mental rotation of hands task (adapted from Sekiyama, 1982).

In this review, I first describe findings about implicit motor imagery. Implicit motor imagery was first suggested from behavioral data in reaction time experiments on mental rotation of the hands, and then explored by using brain imaging techniques. It has been also studied in brain damaged patients. The major brain regions activated for motor imagery are the premotor and parietal cortex, and implicated functions of these areas are described in terms of recent findings in humans and monkeys. Then, we take a look at some recent findings on multi-modal interaction in perceiving tactile stimulation applied to the hands. Finally, plasticity of body schema is considered, including phantom limb phenomena and prism adaptation.

Implicit motor imagery

Mental rotation of the hands

Suppose that you are presented pictures of human hands in various orientations (Figure 1) and asked to identify each of them as a left or right hand. Sekiyama (1982) demonstrated that in this kind of mental rotation task, reaction times systematically vary, not only depending on the rotational angle of stimuli, but also reflecting hand-specific joint constraints. Namely, for each hand, greater reaction times were found for those positions that the arm and the hand cannot easily reach with a real movement (Figure 2). This response pattern revealed a preference for “manageable direction” of actual movements, suggesting that participants’ judgments are based on an internal process that preserves kinesthetic and/or proprioceptive information for the real movements. This finding was confirmed by Parsons (1987), and the internal process is now often called implicit “motor imagery” (Parsons et al., 1995). The finding provides a clue to exploring body schema from which we can generate motor imagery, or mental simulation of movements.

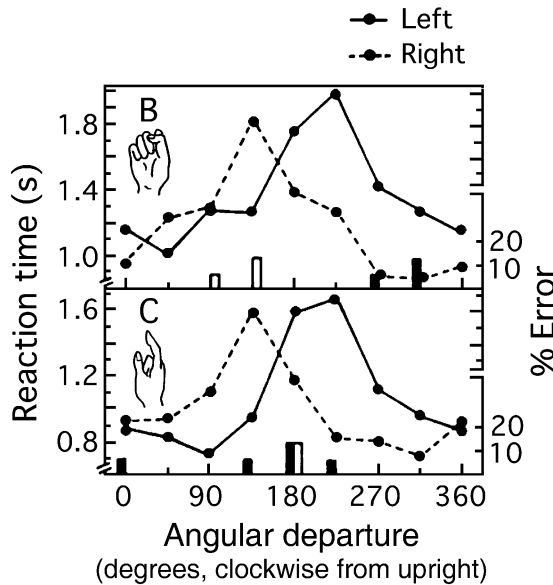


Figure 2. Reaction time function that shows a “manageable direction” of mental rotation of hands (adapted from Sekiyama, 1982).

Interestingly, motor imagery is strongly influenced by the actual position of the participant's hand during the task. In a study by Parsons (1994), participants performed this task in two hand posture conditions: one was palms down (a relatively natural position) on the table, and the other was with the hands back to back, and the sides of the little fingers in front. The participants responded using foot switches. Reaction times were significantly longer for the unnatural hands back to back posture, and this slowing effect was the greatest for stimuli depicting the palm on display. The finding that the current hand position influences perception suggests that the body schema, which enables the visual hand identification task to be carried out, updates its status with the incoming proprioceptive information.

Developmental changes in implicit motor imagery

How crucial is the current hand position to motor imagery compared with the stored "canonical" configuration of hands? In a recent study, Funk, Brugger, and Wilkening (2005) tested children and adults with this hand identification task in two hand position conditions: one was palms down (a natural position for typing), and the other palms up (the keyboard was inverted). Considering the fact that back views of hands are often easier to identify than palm views (e.g., Ashton, McFarland, Walsh, & White, 1978; Sekiyama, 1982), they intended to see if the back versus palm view advantage is a result of the current hand position or because of some canonical representation. Surprisingly, the back view advantage disappeared in the 6-year-old children when their palms were facing up, indicating that the current hand position is crucial. However, in the adult participants, the back view advantage did not disappear, although the advantage decreased in the palm-up condition. These results indicate that: (1) in young children, the current proprioceptive information has a decisive role in motor imagery; and (2) adults' motor imagery is influenced by both a canonical (back view) representation in long-term

memory and the current proprioceptive information.

It appears that young children's motor imagery is not yet obedient to canonical configuration, possibly as a result of more sensorimotor and less symbolic properties of their body schema, as suggested by developmental theorists (Bertenthal & Clifton, 1998; Piaget, 1954). The developmental characteristic found by Funk et al. (2005) was also found in a recent study by Sekiyama (2005), in which children (6-, 7-, 8-, 9-, and 10-year-olds) and adults performed the hand identification task with their hands holding a game controller with a natural back-view posture (both hands were approximately 45° rotated from the upright position toward the midsagittal plane). Reaction times indicated that the starting position of mental rotation was more anchored to the current hand position than the canonical upright representation in the 6- and 7-year-olds, and the influence of the canonical upright representation became obvious after 8 years.

Neuronal basis of implicit motor imagery

In the explosion of studies using brain imaging techniques since the mid-1990s, implicit motor imagery has been used as a tool to explore motor planning processes. Bonda, Petrides, Frey, and Evans (1995) used positron emission tomography to see brain activation specific to mental transformation of the body. They presented photographs of hands in a mental rotation paradigm and scanned participants' brains in two conditions: one was a "hands mental rotation" task in which the participant was asked to identify each stimulus as a left or right hand and respond by clicking one of two mouse keys with the right hand. The other was a "hands control" task, a picture memory task in which stimuli were limited to seven of the familiarized eight hand shapes and the participant was to report the missing one at the end of the scan. The participant was asked to monitor the stimuli by clicking a mouse key with the right hand at each presentation. By subtracting cerebral blood flow in the hands control condition from that in the hands mental rotation condition, activations related

to mental transformation of the body were examined. Activated regions included the parietal association cortex, visual association areas, and motor-related areas such as the premotor cortex. The parietal cortex is essential for spatial judgments and visual attention (Andersen, 1987; Holmes, 1918), and it projects to the premotor cortex through which visuomotor transformation necessary for motor planning takes place (Hoshi & Tanji, 2000; Jeannerod, Arbib, Rizzolatti, & Sakata, 1995; Johnson, Ferraina, & Caminiti, 1993). The involvement of such a pathway indicates that mental rotation of the hands includes the motor planning process equivalent to the real movements. This result was consistent with other reports on motor imagery (Decety et al., 1994; Parsons et al., 1995).

The nature of motor imagery is characterized by comparing mental rotation of the hands with that of non-body objects, such as geometric forms and alphanumeric letters. Whereas mental rotation of the hands results in brain activation of motor-related regions (Bonda et al., 1995; De Lange, Hagoort, & Toni 2005; Kawamichi, Kikuchi, Endo, Takeda, & Yoshizawa, 1998; Parsons et al., 1995; Sekiyama, Miyauchi, Imaruoka, Egusa, & Tashiro, 2000), mental rotation of non-body objects does not (Alivisatos & Petrides, 1997; Cohen et al., 1996; Kosslyn, Digirolamo, Thompson, & Alpert, 1998; Richter, Ugurbil, Georgopoulos, & Kim, 1997). Among cortical regions, mental rotation of the hands essentially depends on the premotor cortex in addition to the parietal cortex, but mental rotation of non-body objects is mostly based on the parietal cortex.³

³ The exact activated regions vary somewhat among studies, for example, some include the dorsal premotor cortex (Brodmann's area 6) and some the ventral premotor cortex (BA44). In this review, these exact regions are not described for the sake of simplicity. Because of variable task contrasts and experimental designs, brain imaging studies can output slightly different results. Also, the correspondence between the monkey brain regions (shown in Figure 4) and those of humans (often described by Brodmann's areas) is not straightforward. It seems important to extract a general tendency from accumulated brain imaging data.

Kawamichi and colleagues (Kawamichi et al., 1998) investigated the time course of brain activation during mental rotation of the hands using magnetoencephalography (MEG). Their results showed that mental rotation of the hands is based on a successive process of activations starting from the visual cortex (~100–200 ms from stimulus onset), followed by those in the inferior parietal lobe (after 200 ms), and then later activations in the premotor cortex that partially overlapped with the parietal activations. This process indicates a transformation sequence of spatial coding from the retinotopic to body-part-centered coding, and then into motor commands. In later sections, we will look at related neurophysiological evidence reported in monkeys.

Laterality on motor imagery

The brain functions show a cerebral laterality in many aspects. Then, like motor execution, is motor imagery of the hand controlled by the contralateral hemisphere?

In a study on split-brain patients, Parsons and colleagues presented a left or right hand randomly to the left or right visual field of the patients for a brief period of time (Parsons, Gabrieli, Phelps, & Gazzaniga, 1998). The two patients had undergone callosal surgeries more than 15 years before the test. The patients could not identify a hand unless its identity was contralateral to the projected hemisphere; that is, they could not identify a right hand presented to the right hemisphere (i.e., left visual field), and vice versa (Figure 3). Thus, for these split-brain patients to correctly identify a visual hand, it needed to be projected to the contralateral hemisphere where its motor execution is controlled. The normal control group did not show such laterality in accuracy, but showed a similar trend in reaction times.

How far and in which brain region is motor imagery lateralized in normal participants? In a positron emission tomography study by Parsons and colleagues (Parsons et al., 1995), healthy volunteers showed that there were activations contralateral to the hand in some motor-related areas including the premotor cortex. However, other studies indicated that,

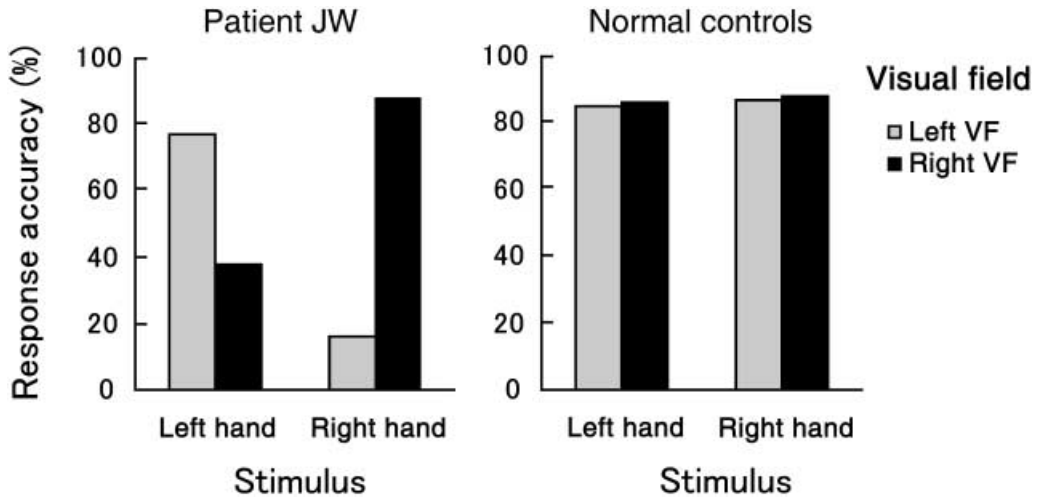


Figure 3. Performance of a split-brain patient in the mental rotation of hands task compared with that of normal controls (adapted from Parsons et al., 1998).

for the same hand identification tasks, activations in the premotor cortex tended to be bilateral, with some dominance of the left hemisphere (Kawamichi et al., 1998, MEG; Sekiyama et al., 2000, functional magnetic resonance imaging). Thus, in the premotor cortex, contralateral control of motor imagery remains to be proved although the notion is consistent with electrophysiological findings on motor execution in monkeys (Wise, Boussaoud, Johnson, & Caminiti, 1997).

In patient studies, such contralaterality in motor imagery has been demonstrated in the parietal cortex. Parietal lobe lesions often produce apraxia, an impairment of skilled movements, in the absence of elementary sensory or motor deficits, suggesting a relationship with motor imagery deficits. Sirigu and colleagues (Sirigu et al., 1996; Sirigu & Duhamel, 2001) found that posterior and superior parietal lesions lead to a deficit of imagining contralesional hand movements, which is dissociated from motor execution deficits. The imagery deficit was limited to the contralesional hand in right parietal lesion patients. Consistent with the observation that left parietal lesions can produce bilateral apraxia, left parietal lesion patients tended to show the imagery deficit for both hands. These results indicate

that the parietal cortex is important for simulated hand movements, particularly for motor imagery of the contralateral hand at least in the right hemisphere.

Motor imagery in upper limb amputees

As we saw in the earlier section, motor imagery is based on both current sensory input and stored body representation. What happens to motor imagery if a limb is lost surgically or accidentally? Upper limb amputees lack sensory input from the missing hand, but they still have a cortical (somatosensory) representation of the hand, which supposedly causes phantom limb sensations, that is, vivid kinesthetic sensations as if the missing hand still exists.

Nico and colleagues (Nico, Daprati, Rigal, Parsons, & Sirigu, 2003) tested 16 upper limb amputees with mental rotation of the hands. The amputees were less accurate and slower than normal control participants in this hand identification task. However, their performances varied depending on orientation and view of the hand in the same way as in the controls, indicating that the amputees could still mentally simulate hand movements although the process was deteriorated. The deterioration was more severe in amputees of the dominant

hand than those of the non-dominant hand. Interestingly, experience of wearing a prosthetic hand interfered with the simulated movements, with the greatest performance deterioration in amputees of the dominant hand who wore a prosthesis. Amputees of the non-dominant hand that did not wear a prosthesis performed at almost the same level as the normal controls. These results suggest that the amputees still preserve a body schema that is essentially the same as that of the normal control, but its efficiency deteriorates especially following the loss of the dominant hand, and that wearing a prosthesis daily contributes to the deterioration. We will return to this topic later in relation to the phantom limb phenomena.

Multimodal perception of hands and hand movements

As we have seen, the major brain regions activated for motor imagery are the premotor and parietal cortices. Recent findings in neurophysiology, neuropsychology, and psychology work together to show that these areas are particularly important for perceiving the body and body actions. The findings also revealed multimodal integrative functions of these areas, suggesting their roles for body schema.

Bimodal neurons in the monkey premotor and parietal cortex

Graziano, Gross, and their colleagues have demonstrated that neurons in the ventral premotor cortex (PMv) of the monkey encode the locations of stimuli with respect to body parts, such as the arm and head (Graziano & Gross, 1995; Graziano, Hu, & Gross, 1997; for a review, see Graziano & Gross, 1998). The PMv receives sensory input from the parietal lobe and can influence movement through its projections to the primary motor cortex and the spinal cord (see Figure 4). Most PMv neurons respond to tactile stimuli, and many of them also respond to visual stimuli placed near the tactile receptive field. In these bimodal neurons, if their tactile receptive fields are on the arm, they respond to visual stimuli adjacent to the arm.

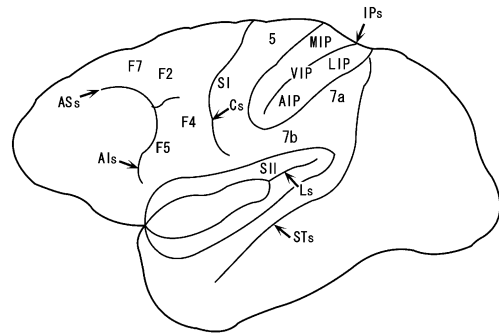


Figure 4. A functional map of the monkey brain (adapted from Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). According to this map, the ventral premotor cortex consists of F4 and F5, and the dorsal premotor cortex F2 and F7. AIP, anterior intraparietal area; Als, inferior arcuate sulcus; ASs, superior arcuate sulcus; Cs, central sulcus; IPs, intraparietal sulcus; LIP, lateral intraparietal area; Ls, lateral sulcus; MIP, medial intraparietal area; S1, primary somatosensory area; SII, secondary somatosensory area; STs, superior temporal sulcus; VIP, ventral intraparietal area. (IPs and Ls have been opened to show hidden areas.)

When the arm is moved, the visual receptive fields also move (Figure 5), but when the eyes move, these visual receptive fields do not move. That is, the visual receptive fields of the bimodal neurons are not in retinocentric coordinates, but in arm-centered coordinates. The arm-related bimodal neurons in the PMv are active during movements of the arm, and electrical stimulation of these neurons causes arm movements (Gentilucci et al., 1988). Thus, the PMv seems to contribute to sensory-motor coordination through its tight spatial relationship with the body parts performing that movement. From their bimodal nature, they also contribute to visual-proprioceptive integration (e.g., Graziano, 1999).

Bimodal neurons have been discovered in several brain regions so far, including the PMv (area F4; Graziano & Gross, 1995; Rizzolatti, Scandolaro, Matelli, & Gentilucci, 1981), parietal cortex (Hyvarinen & Poranen, 1974), intraparietal sulcus (Duhamel, Colby, & Goldberg, 1998), superior temporal sulcus (Bruce, Desimone, & Gross, 1981; Hikosaka,

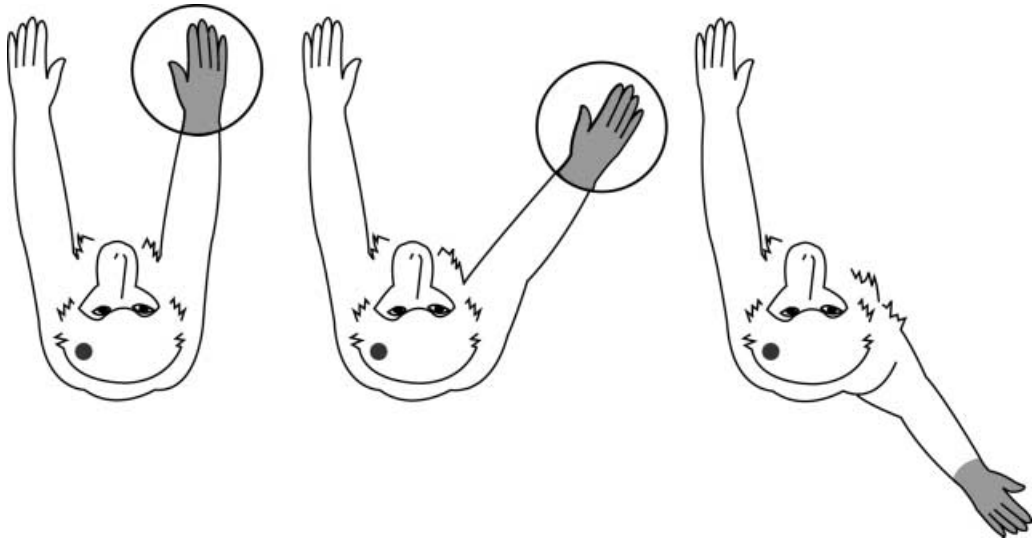


Figure 5. A schematic display of the visual receptive field (circled) of an arm-centered neuron in the ventral premotor cortex (adapted from Graziano & Gross, 1995). In this neuron, no visual responses are elicited when the arm (tactile receptive field is shaded) is not in the space in front of the body.

Iwai, Saito, & Tanaka, 1988), putamen (Graziano & Gross, 1995), and superior colliculus (Stein & Meredith, 1993). Some of these areas might be of close relationship with the “mirror neuron” system, a cortical network including the PMv (monkey area F5), inferior parietal cortex (area PF or 7b), and superior temporal sulcus (STSa), which has been proposed as a system for action recognition (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996, 2002; Rizzolatti, Fogassi, & Gallese, 2001). Mirror neurons, originally found in area F5 of monkeys (Figure 4), are activated during the execution of purposeful, goal-directed hand movements, and they also discharge when the monkey observes similar hand actions performed by other individuals (Gallese et al., 1996). The activation of these neurons requires visual stimuli of interaction between the action’s agent (human being or monkey) and the object to be manipulated. These findings have motivated a wide range of studies on social functions of mirror neurons beyond the scope of this review (see Murata, 2005; for a review).

Interestingly, it may be possible to educate unimodal neurons to be bimodal neurons through visuomotor experience. Obayashi, Tanaka, and

Iriki (2000) trained monkeys to retrieve a food reward with their hand on a table under a plate that can be turned transparent or opaque (Figure 6) until the monkeys could retrieve the food under the opaque plate (thus, with the hand invisible). After the training, in the anterior bank of the ventral intraparietal sulcus (Figure 4), where neurons were essentially somatosensory at the beginning, a group of bimodal neurons exhibited clear visual responses. When these neurons were examined with the hand placed in different positions under the opaque plate, the visual receptive fields of the now bimodal neurons clearly “followed” the position of the invisible hand. These results indicate that the experience of associating visual and proprioceptive information can turn somatosensory neurons into bimodal ones, and that such an experience may enable the monkey to generate visual imagery of the invisible hand.

Bimodal neurons and body schema

Among the various brain regions containing bimodal neurons, the parietal cortex seems of particular importance for body schema. Graziano and colleagues found that neurons in parietal area 5 of the monkey brain respond even to

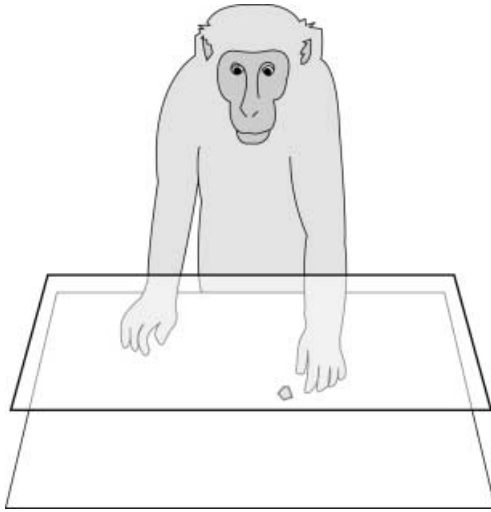


Figure 6. The equipment used to make the arms invisible during training of a monkey to take food. The plate (made of liquid crystal) covering the arms could be changed to transparent or opaque (adapted from Obayashi et al., 2000). After this training, a group of neurons in the ventral intraparietal sulcus, which were originally somatosensory, began to respond to visual stimuli.

the sight of a realistic fake arm when it is presented in appropriate positions (Graziano, Cooke, & Taylor, 2000; also see Graziano & Botvinick, 2002). They chose area 5 neurons that respond to the sight of the arm of the monkey. Then, the monkey's arm was covered and a realistic fake arm was visually presented (Figure 7a,b). Many of these neurons were influenced by the sight of the fake arm, with their activity enhanced when both the felt (real arm) and seen (fake arm) positions were on the neuron's preferred side (Figure 7a). Such enhancement was not observed when non-body objects were presented, or when the fake arm was presented in non-realistic orientations (e.g., when a fake left arm was presented at the position of the right hand, as in Figure 7b). Surprisingly, the neurons are able to distinguish a left arm from a right arm on sight. These results suggest that neurons in area 5 integrate proprioceptive and visual position cues when the visual cues match the

body schema of the monkey. In contrast, neurons in the primary somatosensory cortex (S1) were not influenced by the fake arm at all. Therefore, in the ascending somatosensory pathway from the periphery to area S1 and to area 5, the first stage of somato-visual integration about arm position is likely to be in area 5 (Figure 4). Because parietal area 5 is thought to receive the efference copy from the primary motor cortex (Kalaska, Caminiti, & Georgopoulos, 1983), this area seems particularly relevant to body schema.

Multimodal perception of peripersonal space

Parallel to the investigations of bimodal neurons, there has been a growing interest in multimodal perception of body parts and peripersonal space immediately around the body parts in humans. By using a crossmodal congruency effect, Driver, Spence, and their colleagues have shown a convergence of visual and tactile cues by behavioral measure (Maravita, Spence, & Driver, 2003; for a review). To demonstrate this effect, the participant is provided with vibrotactile stimulation on the thumb or index finger and asked to judge the location of the stimulus, by making up-down (i.e., finger-thumb) discrimination with foot switch responses. Concurrently, a visual distractor (a light) is presented from one of the four possible locations of a tactile stimulus (Figure 8a,b). It is known that incongruent visual distractors (e.g., an upper light during lower touch) interfere with tactile judgments, especially when the irrelevant light appears close to the stimulated hand. The interfering effect is measured by the performance difference between incongruent versus congruent trials, which is called a crossmodal congruency effect. Critically, if hands are crossed, this effect "follows" the hand, like the responses of bimodal neurons.

Multimodal perception of body parts

To investigate the roles of visual and proprioceptive inputs in the perception of body parts, Pavani, Spence, and Driver (2000) used "rubber hands" in a modified version of the

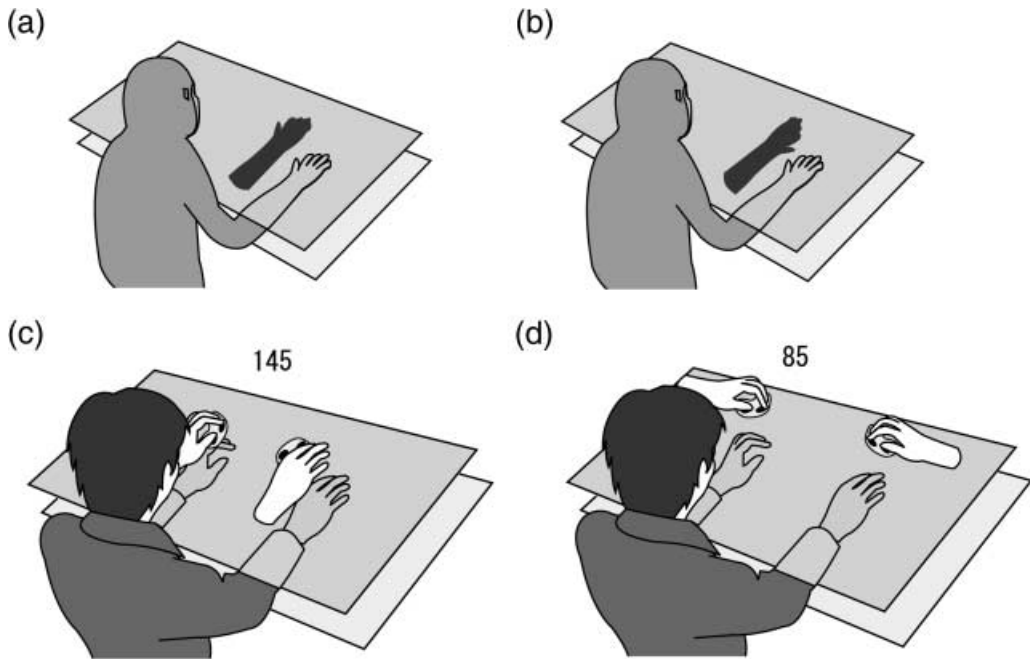


Figure 7. Effects of the sight of a rubber arm that matched or did not match the body schema on multimodal perception of body parts. The upper panels (a,b) schematically show how to test the monkey parietal neurons (for Graziano et al., 2000). The numbers in the lower panels (c,d) show the crossmodal congruency effect in humans, the impact of visual distractors on tactile performance in milliseconds, and differences between the incongruent and congruent trials for each hand (adapted from Maravita, Spence, & Driver, 2003).

crossmodal congruency task. The hands of participants were covered by an opaque plate and stuffed rubber gloves were visually presented on the plate (Figure 7c,d). Visual distractors (lights) attached to the rubber hands elicited a significantly larger crossmodal congruency effect compared with the effect in the absence of the rubber hands. But such an enhancement did not occur when the rubber hand position was not aligned to the invisible position of the real arm. Thus, like monkey bimodal neurons (Graziano, 1999; Graziano et al., 2000), the seen “virtual hand” seems to be integrated with proprioceptive information only when it matches the body schema. The effect of the aligned rubber hand can be also shown by using simple pictures of hands instead of rubber hands (Igarashi, Kitagawa, & Ichihara, 2004).

Tool-use experience

The peripersonal space in which the crossmodal congruency effect occurs can be enlarged when the participant holds a tool in the hand (Maravita, Spence, Kennett, & Driver, 2002). The crossmodal congruency effect can be elicited between visual distractors at the tip of the tool and the tactile targets at the hand. More importantly, increasing the experience in using the tool seems to produce further modification in peripersonal space. For example, the spatial constraints on the crossmodal congruency effect can be reversed when the tools are crossed (Figure 8c,d). Thus, the space for visuo-tactile interaction “follows” the tool in the hand after the person has become accustomed to using it.

The influence of tool-use has also been demonstrated at the neurophysiological level. Iriki and colleagues (Iriki, Tanaka, & Iwamura,

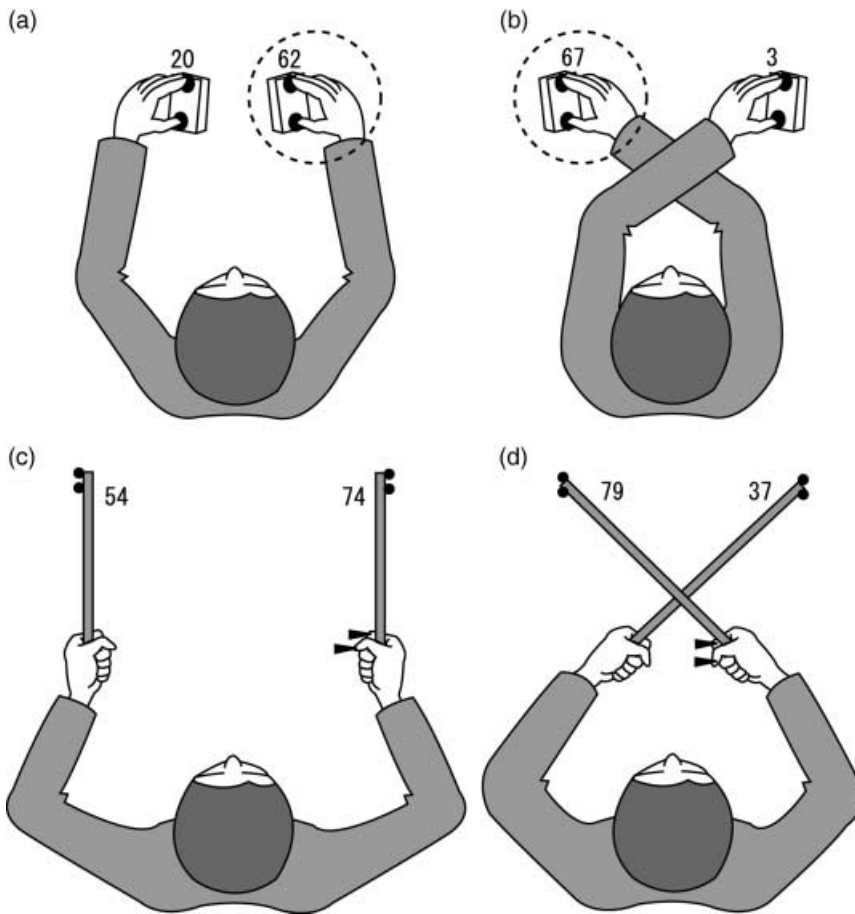


Figure 8. Behavioral consequences of posture changes on the crossmodal congruency effect (adapted from Maravita et al., 2003).

1996) recorded parietal neurons in monkeys that had become skilled in using a long rake as a tool to extend reachable space. After a few minutes of using the tool as a “warm-up,” a remarkable neuronal modulation was observed in bimodal neurons in the anterior bank of the intraparietal sulcus. Namely, these neurons started to respond to visual stimuli near the far end of the tool, thus the visual receptive fields were enlarged along the axis of the tool. But such enlargement was not observed when the monkey did not intend to retrieve the food with the tool, even if the monkey kept holding the tool. It seems that these parietal neurons are triggered by a motor plan to incorporate a tool into the body schema.

Modification of body schema

Adaptation to displaced vision

Prisms have often been used to investigate the relationship between visual and proprioceptive information in perceiving hand location (Welch, 1986). For example, a wedge prism displaces the visual field laterally to the left or right. When the participant points to targets viewed through the prism, s/he initially misreaches in the direction of the displacement. After continued experience of looking through a prism while moving the hands, not only does reaching become accurate, but perceptual adaptation occurs. If the adapted participant is asked to close their eyes and point straight

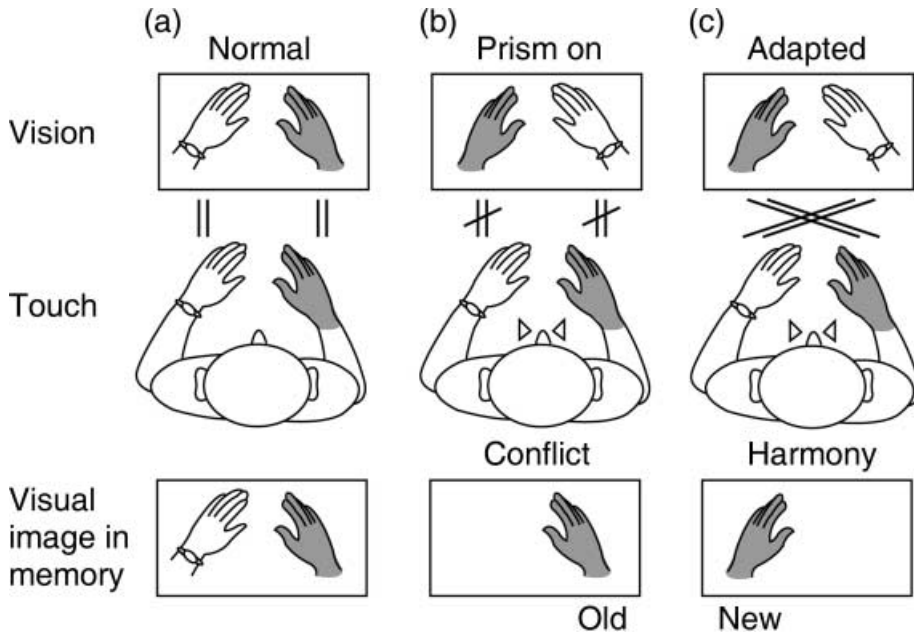


Figure 9. Effects of prism adaptation to reversed vision on perceiving and imagining one's own hands (from Sekiyama et al., 2000, *Nature* Vol. 407). When first wearing the reversing spectacles, the seen and felt hands elicit a perceptual conflict, but after prolonged adaptation, they become in harmony. Like the experience of crossed tools, connections between the seen and felt hands are learned and stored so that imagined hand could look reversed.

ahead with the adapted hand, s/he tends to misplace the hand off the body midline in the direction opposite to the prism displacement. The adaptation indicates a recalibration of the relationship between the visual and proprioceptive spatial coordinates. Brain regions related to this recalibration have been found in the parietal (Clower et al., 1996), premotor cortex (Kurata & Hoshi, 1999), and cerebellum (Jeannerod & Rossetti, 1993) so far.

Rossetti and colleagues (Rossetti et al., 1998) questioned if such a recalibration process improves rehabilitation of hemispatial neglect in parietal damaged patients. One motivation for this question was that a basic feature of the neglect resulting from right parietal damage (thus, neglect of the left-side space) is a pathological shift of the subjective midline to the right. After a short period (50 pointing trials) of prism adaptation for displaced vision to the right, the left hemispatial neglect patients showed a shift of the subjective midline to the

left (in the direction that cancelled the pathological shift) when tested with eyes closed. Moreover, they also showed general improvement of visuomotor performances in classical neuropsychological tests, such as copying objects. Since then, prism adaptation has been shown to improve several visuospatial neglect symptoms, including visuomotor tasks (e.g., Frassinetti, Angeli, Meneghello, Avanzi, & Ladavas, 2002) and contralesional tactile perception (Maravita et al., 2003). It seems that the process of prism adaptation includes not only arm-specific visual-proprioceptive recalibration, but also reorganization of higher levels of spatial representation (see also Malhotra, Coulthard, & Husain, 2006; Redding & Wallace, 2006).

Adaptation to reversed vision

When viewed through a left-right reversing prism, an actual right hand is seen as a left hand (Figure 9b). Thus, if a participant moves

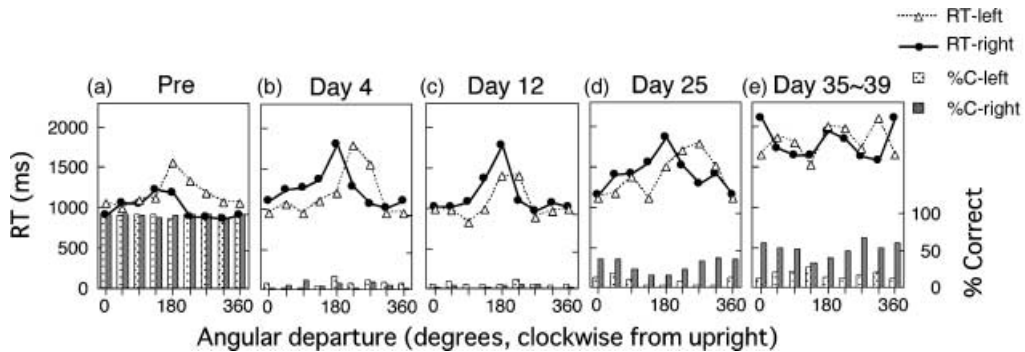


Figure 10. Performances in mental rotation of the hands during adaptation to reversed vision (reproduced from Sekiyama et al., 2000). Correct responses reappeared after 3 weeks of adaptation. It was earlier for the dominant (right) hand in familiar orientations.

the actual right hand to the right, s/he will see a left hand moving in the left visual field, and this will initially cause perceptual conflict between the seen and felt hands. Even with such a drastic transformation, after a prolonged adaptation period, humans and monkeys are known to adapt with remarkable flexibility (Kohler, 1964; Miyauchi et al., 2004; Sekiyama et al., 2000; Sugita, 1996). It has been suggested that seeing one's own hands and body is crucial for adaptation (Kohler, 1964; Sekiyama, 1997; Stratton, 1897).

Sekiyama and colleagues (Sekiyama et al., 2000) investigated the participants' body image during 5 weeks of continually wearing left-right reversing spectacles. They asked participants to identify pictures of hands presented in a mental rotation paradigm as a left or right hand. Early in the prism-wearing period, correct responses essentially disappeared because of the reversed appearance of the visual stimuli. However, after 3 weeks of adaptation, correct responses reappeared, suggesting the emergence of a new hand representation (Figure 10). There were more correct responses for right-hand stimuli (dominant hand), especially in prototypical orientations. This indicates that in the participant's body schema, new hand representation is generated earlier for the dominant hand in its most familiar orientation. The non-perfect accuracy suggests a coexistence of the new and old hand representations in body schema. The adaptive modification

in hand representation was also suggested in the left-right discrimination of the location of a visual target on a display, for which responses were made by either the left or right invisible hand. In this visual localization task, correct responses reappeared also in the fourth week. Taken together, it was inferred that the new hand representation contains reversed mapping between visual and motor/proprioceptive coordinates (Figure 9c). If the reversed mapping operates on visual input coming through the prism, it would produce normal motor output and would therefore virtually cancel out the reversal of visual input. Such a mechanism is plausible at least within the space for hand actions, as we have seen neurophysiological evidence for the body-part centered space coding.

Phantom limb and brain plasticity

Phantom limb is a syndrome that most limb amputees undergo, where they experience vivid somesthetic sensations as if the missing limb were still present (Mitchell, 1872). The syndrome emerges immediately after amputation, and it may persist for years. Despite a pile of literature on clinical phenomenology of the syndrome, a systematic scientific study on the phantom limb began only recently, inspired mainly by the demonstration of striking changes in somatosensory maps in animals following denervation or amputation (Ramachandran & Hirstein, 1998; for a review).

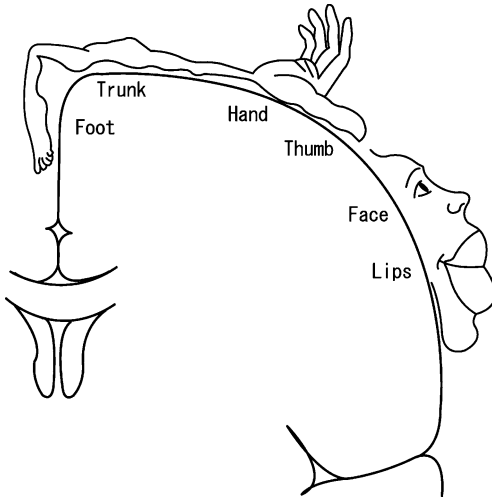


Figure 11. Penfield map of the primary somatosensory cortex (adapted from Penfield & Rasmussen, 1955). Note that the hand area is bordered by the face area on one side, and by the upper limb on the other side. The hand and upper arm areas “invade” the hand area following amputation of the arm.

It is known that the primary somatosensory cortex of primates contains a complete somatotopic map of the body surface, often called the Penfield map (Penfield & Rasmussen, 1955; Figure 11; for monkeys, see Merzenich et al., 1984). Apparently, this cortical map is genetically determined, but a remarkable experiment by Pons and colleagues (Pons et al., 1991) found that after long-term deafferentation of one upper limb, the cortical area originally corresponding to the hand is taken over by sensory input from the face and the cells in the “hand area” start responding to stimuli applied to the lower face region (also see Florence, Taub, & Kaas, 1998; Jones & Pons, 1998; Merzenich, 1998).

Inspired by this finding, Ramachandran and colleagues have found the same reorganization in human amputated patients (Yang et al., 1994; Ramachandran & Hirstein, 1998). Their findings included the following: (1) in approximately half of the patients studied, tactile input from the lower face was often perceptually mislocated on the phantom arm; and (2) MEG measurement of amputees confirmed

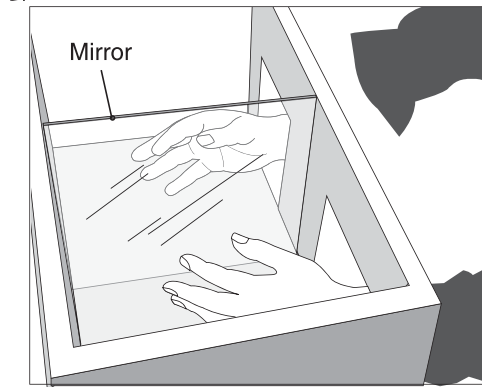


Figure 12. A mirror device used to promote “voluntary movements” of the phantom limb (adapted from Ramachandran & Hirstein, 1998). By creating a visual illusion of the missing hand as a mirror image of the normal hand, most patients could easily move the phantom hand.

that the tactile input from the face could elicit brain activations in the hand area of the somatosensory cortex, in addition to those in the face area. Moreover, their perceptual and MEG data showed that the hand area in the Penfield map was flanked on one side by the face and on the other side by the upper limb (the residual part of the amputated arm). These results indicate that because of the loss of sensory input from the hand, the cortical hand area of the amputee is invaded by the neighboring areas to a large extent (Figure 11). It is surprising that such a massive reorganization takes place even in the adult brain.

Another remarkable finding on the phantom limb is its interaction with visual input. Upper limb amputees often report that the phantom is impossible to move voluntarily. Ramachandran and Rogers-Ramachandran (1996) demonstrated that such paralysis can be resolved by giving a visual illusion of the missing hand. A tall mirror was placed vertically on a table in such a way that the patient could see the reflection of his/her normal hand “superimposed” on the phantom hand (Figure 12). When the normal hand was moved it provided a visual image of the missing hand, and most

patients could voluntarily move the phantom hand with a vivid kinesthetic sensation. They could not move the phantom hand voluntarily with the eyes closed, indicating the strong influence of the concordant visual information on the phantom kinesthetic sensation. Notably, because of the visual illusion of the missing hand, one patient experienced the phantom kinesthetic sensation for the first time after amputation. Taken together, the phantom limb sensation must be based not only on the somatosensory cortex, but also on higher areas, such as the parietal association cortex where visual and somatosensory information converges.

As described earlier, to solve the mental rotation of the hands, upper limb amputees performed similarly to normal controls, but with less efficiency in motor imagery (Nico et al., 2003). This result and the finding from the mirror experiment (Ramachandran & Rogers-Ramachandran, 1996) suggest that body schema of arm amputees is essentially preserved in their normal state although it is somewhat weakened. The deterioration of motor imagery was largely associated with the experience of wearing a prosthesis on the dominant hand. From the frequency and precision of its movements, the dominant hand must be represented more extensively in the brain than the non-dominant hand. If the dominant hand is lost, the influence could be substantial. Moreover, an aesthetic prosthesis, which cannot be manipulated like a real hand, and thus does not match the body schema, will critically interfere with motor imagery of the dominant hand.

Concluding remarks

The classical notion of body schema (Head, 1918) has often been used as an explanatory concept rather than a problem to be studied. However, there has been substantial progress in the study of body schema, with recent advances in experimental methodology and techniques.

Mental rotation of hand shapes can be used as a tool to investigate body schema. Research has shown that the back view is a canonical configuration of hands, and adults' motor

imagery is influenced by both a canonical representation in the long-term memory and current proprioceptive information. Apparently, the body schema consists of a relatively persisting component and a variable component to be updated. The persisting canonical component may not be established well in young children. But once established, it may not be deleted even after an arm is amputated, although it can be somewhat weakened. Neuroimaging studies have shown that motor imagery is related to a pathway including the parietal association cortex and premotor cortex, indicating that a process of visuomotor transformation is involved.

Converging evidence from animal and human studies suggests that the peripersonal space immediately surrounding body parts is recognized by body-part-centered spatial coordinates that integrate visual, tactile, and proprioceptive information, and perhaps motor plans. The body-part-centered space coding has been found in several brain areas, and the connection between the parietal association cortex and premotor cortex may be particularly important for recognizing the space around the arm.

After a certain period of tool use, the body schema can be enlarged so that the tool is incorporated into it. Modification of the body schema also occurs after adaptation to prismatic vision. After adaptation to displaced vision, recalibration occurs in the relationship between visual and proprioceptive spatial coordinates. After adaptation to reversed vision, a new hand representation is added to the body schema, such as a tool.

The cortical representation of the body in the somatosensory cortex can be modified after amputation of an arm. But such a modification does not mean a total loss of body image of the arm. Visual input can be triggered to regain the body image (i.e., kinesthetic sensation of a phantom limb), interacting with some somatosensory pathway, perhaps in the parietal association cortex.

These findings help to specify properties of the body schema, its components, functions, and modifiabilities. We now have various clues to investigate body schema.

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