6 How the brain represents the body: insights from neurophysiology and psychology

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Abstract. To reach for the computer mouse, to sit upright in a chair or hold a journal in order to read it, indeed, to do most of the actions that we commonly perform, we rely on a representation of the spatial configuration of the body. How and where in the brain is the body represented and what are the psychological properties of this body schema? In this article we review first the neurophysiology and then the psychology of the body representation. One finding that has emerged from both approaches is that the body representation is not merely a registration of proprioceptive inputs about joint angle. Instead, the brain contains a sophisticated model of the body that is continually updated on the basis of multimodal input including vision, somesthesis, and motor feedback. Neurophysiological studies in the monkey brain show that parietal area 5 is a critical node for processing the body's configuration. Neurons in area 5 combine signals from different modalities in order to represent limb position and movement. Psychological studies show that the body schema is used to cross-reference between different senses, as a basis for spatial cognition and for movement planning.

> I thrust my arms wildly above and around me in all directions. I felt nothing . . . I cautiously moved forward, with my arms extended, and my eyes straining from their sockets . . .
>
> Poe, *The Pit and the Pendulum*

> Sometimes, too, just as Eve was created from a rib of Adam, so a woman would come into existence while I was sleeping, conceived from some strain in the position of my limbs.
>
> Proust, *Swann's Way*

> 'Easy!' I said. 'Be calm! Take it easy! I wouldn't punch that leg like that.'
> 'And why not!' he asked, irritably, belligerently.
> 'Because it's your leg,' I answered. 'Don't you know your own leg?'
>
> Sacks, *The Man who Mistook his Wife for a Hat*

6.1 Introduction

Without an internal representation of the body, a mental model of the relative positions of the head and limbs, we would be unable to perform the most vital or trivial actions; unable to move toward and around the objects that surround the body; unable to process the locations of those objects in relation to the body; disoriented and without any sense of physical self. In the first quote above, the protagonist of the story tries to understand the layout of his environment by touch and by use of his body representation. A touch on his hand will do him no good unless he knows the position of his outstretched arm. In the second quote, the position of the limbs implies the presence and shape of a nearby object. The third quote is about a brain-damaged patient whose internal body representation no longer includes his own leg.

The internal representation of the body has been studied on two different disciplinary fronts: a neurophysiological one and a psychological one. Until recently, these two approaches were surprisingly isolated from each other. The psychological approach emphasized the multisensory nature of the body representation. This work demonstrated that vision, touch, and proprioception are combined and cross-referenced in a sophisticated mental schema of the body. Neurophysiology, in contrast, emphasized proprioception, one component of body representation, and focused especially on the use of proprioception in the control of movement. Only recently have these two fields become more integrated and begun to converge on similar themes. The psychological studies have turned more toward exploring the spatial coordinate systems that organize the representation of the body and the control of movement. In neurophysiology, recent experiments have focused on how vision, proprioception, and touch are integrated by single neurons in the parietal lobe and premotor cortex.

The purpose of the present article is to review both areas of research side by side, providing an overview of each and describing some of the relations between the two. The first half of the article reviews neurophysiological studies on body representation, mainly in the monkey brain. These experiments examine a set of interconnected somatosensory and motor brain areas, emphasizing area 5 in the superior parietal lobe. The second half of the article reviews the psychological data, emphasizing how the body representation coordinates information within and across perceptual modalities. Both parts of the review share certain underlying themes: the representation of the body is multimodal, and it has a close relationship to the representation of space around the body and the control of movement through that space.

6.2 The neuronal basis of the body representation

6.2.1 Proprioceptive pathways from the periphery to area 5

Proprioception begins in receptors primarily in the joints and muscles (for review, see Burgess, Wei, Clark, and Simon 1982; Iggo and Andres 1982). Information about muscle stretch and joint angle is then transmitted through the dorsal column nuclei of the medulla and the ventrobasal complex of the thalamus, to two principal regions of the cerebral cortex, area SI on the postcentral gyrus and area SII in the lateral sulcus (for a review of these pathways, see Mountcastle 1984). Of these two cortical areas, SI is far better studied and understood, perhaps partly because it is on the top of the brain and easier to reach with a recording electrode.

In area SI information from deep, proprioceptive receptors arrives mainly in the subregions termed 3a and 2, while information from the cutaneous receptors arrives mainly in subregions 3b and 1 (Kaas, Nelson, Sur, Lin, and Merzenich 1979; Mountcastle 1984). These subdivisions of SI contain even smaller partitions, cortical columns a few millimeters wide, that receive information from only one receptor type. Information-processing columns, now known to exist all over the cortex, were first discovered in SI (Kaas *et al.* 1979; Mountcastle 1997).

SI projects to a wide range of cortical sites including area 5 in the superior parietal lobe. All four subregions of SI project to area 5, but the strongest projection is from subregion 2 (Pandya and Kuypers 1969; Pearson and Powell 1985; Vogt and Pandya 1978). That is, area 5 receives input mainly from the deep, proprioceptive receptors. Most of the work on body representation in the

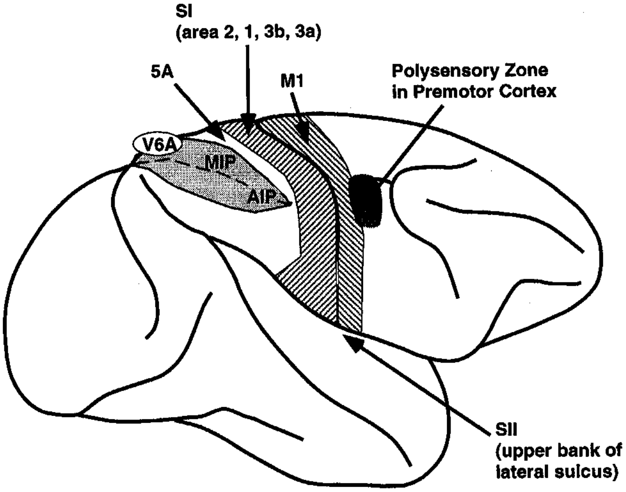


Fig. 6.1 Side view of the macaque monkey brain showing some of the cortical areas involved in representing the physical configuration of the body. The intraparietal sulcus is shown opened up to expose the buried cortex (stippled area). MIP = medial intraparietal area, AIP = anterior intraparietal area, 5A = anterior area 5, M1 = primary motor cortex, SI = primary somatosensory cortex, SII = second somatosensory cortex.

monkey brain has concentrated on area 5. This cortical area is not uniform. As shown in Fig. 6.1, it has several subdivisions, including area MIP on the medial bank of the intraparietal sulcus, V6A on the anterior bank of the parieto-occipital sulcus, a newly suggested area PRR that may overlap V6A and MIP, and a region on the gyral surface termed here Anterior 5 or 5A. Until recently, however, most of the work on area 5 did not distinguish between these different regions.

The following sections review the effects of lesions to area 5, its physiology, and its possible role in body representation and the control of movement.

6.2.2 Lesions to area 5

In 1884, Ferrier and Yeo reported the effects of parietal lesions in monkeys (see Gross 1998 for a review of the history). They argued that visual cortex must be located in the parietal lobe and not the occipital lobe, because monkeys with parietal lesions were unable to reach accurately for pieces of food. Some time after, Balint (1909) observed similar behavior in humans with damage to parietal cortex. Balint and others (e.g. Holmes 1918) realized that the deficit was probably one of sensory-motor integration, spatial attention, or body representation, not vision.

Since then, the parietal lobe syndrome in all its spatial, motor, and attentional manifestations has been studied extensively in humans and monkeys (Andersen 1987; Critchley 1953; De Renzi 1982; Holmes 1918; Kolb and Whishaw 1990; Newcombe and Ratcliff 1989). One of the many deficits often seen in human patients is a disturbance of body representation. For example, some patients will neglect one side of the body, failing to shave or dress on that side; other patients will notice the limbs contralateral to the damaged parietal lobe readily enough, but will mistakenly think that the limbs are not attached to them and belong to someone else. Whether these deficits are associated with one or another subregion of the parietal lobe is difficult to tell in humans, because of the size and uncertain borders of the lesions. Some of these deficits in body representation are discussed further in the second half of this chapter.

Lesions to the superior parietal lobe in monkeys cause deficits in almost all aspects of somesthesis, not just body representation but touch as well (Ettlinger and Wegener 1958; Moffet and Ettlinger 1970; Ridley and Ettlinger 1975; Ruch, Fulton, and German 1938). Murray and Mishkin (1984) argued that many of these deficits were the result of accidental damage to SI itself, not to area 5. Their results indicated that lesions carefully restricted to area 5 had minimal effects on texture, roughness, and shape discrimination. In contrast, lesions to areas SI and SII had a devastating impact on all of these behaviors. They proposed that area 5 processes the spatial component of somesthesis, such as the position of the arm, while area SII processes the perceptual, object-recognition, and memory component of somesthesis that comes with feeling an object with the hand. This dichotomy of the somatosensory system was proposed as a parallel to the visual system. In 1982, Ungerleider and Mishkin proposed that the cortical visual system was divided into two components of which the 'dorsal stream' subserves spatial vision and the 'ventral stream' subserves object recognition and memory. In the view of Murray and Mishkin (1984), area 5 is the dorsal stream, or spatial module of the somatosensory system. Several recent studies by Passingham and colleagues (Rushworth, Nixon, and Passingham 1997a,b) confirmed that area 5 is necessary for the accurate spatial guidance of the arm, especially in the dark when only somatosensory cues are available.

In the next several sections, we describe the properties of single neurons in area 5 and discuss how they might encode the spatial configuration of the body and help to control movement.

6.2.3 Early single neuron studies of area 5

In 1971, Duffy and Burchfiel studied the activity of neurons in area 5 of awake monkeys. They found that most neurons responded to proprioceptive signals—to joint angle and muscle stretch. These cells had highly complex properties. Some combined a tactile receptive field on the skin with a response to joint rotation. Some responded to rotation of more than one joint, and many had bilateral responses. This convergence of different joints and different somatosensory submodalities onto individual neurons was never seen in SI. Typically, neurons in SI have small receptive fields on the contralateral side of the body, and respond to stimulation of one class of peripheral somatosensory receptor only. The differences between area 5 and SI led Duffy and Burchfiel to suggest that area 5 represents a higher stage in somatosensory processing, and especially in the processing of body representation.

Sakata *et al.* (1973) confirmed and extended these findings in area 5. These authors made two important original observations, both of which have been largely neglected. First, they found a subset of area 5 neurons that responded to a touch on the hand, but only if the joints of the arm were placed in certain positions. They argued that such neurons would be able to encode the spatial location of a felt object. Second, they found neurons 'which responded to certain visual as well as to somesthetic stimuli.' This visual input has never been systematically studied, although it was noted by other investigators (Colby and Duhamel 1991; MacKay and Crammond 1987; Mountcastle *et al.* 1975).

Mountcastle and colleagues (1975) provided the first coherent view of the functions of area 5 and its role in behavior. This landmark paper described the properties of neurons in both area 5, in the superior parietal lobe, and the adjacent area 7 in the inferior parietal lobe. In addition to confirming the findings of previous studies, this study made the novel discovery of motor functions in the parietal lobe. In area 5, some of the neurons that responded during passive movement of the arm showed greater response when the monkey moved its arm on its own volition. Some neurons showed no somatosensory activity at all, responding only during the monkey's goal-directed reaches. Another class of neurons responded when the monkey grasped or manipulated objects with its fingers. In area 7, neurons responded in association with eye movement. Some responded during active fixation, others during saccadic or smooth pursuit eye movements. In the words of the authors, 'These regions receive afferent signals descriptive of the position and movement of the body in space, and contain a command apparatus for operation of the limbs, hands and eyes within immediate extrapersonal space.'

The sensory–motor command hypothesis of Mountcastle *et al.* was controversial at first, especially as applied to area 7 (e.g. Robinson, Goldberg, and Stanton 1978), but in the past 20 years has gradually gained a qualified acceptance. Areas 7 and 5 have now been parceled into more than 10 functionally different areas (for review, see Andersen, Snyder, Bradley and Xing 1997; Colby and Duhamel 1991). Some of these areas are involved in eye movement and fixation, such as LIP and V6A (Andersen, Bracewell, Barash, Gnadt, and Fogassi 1990; Galletti, Battaglini, and Fattori 1995; Nakamura, Chung, Graziano, and Gross 1999). Some parietal areas are more involved in arm movement, such as areas MIP, PRR, and 7 m (Colby and Duhamel 1991; Ferraina *et al.* 1997; Snyder, Batista, and Andersen 1997). Parietal area AIP may be involved in grasping objects with the hand (Sakata and Taira, 1994). Even in the human literature, the parietal lobe has come to be viewed as a sensory–motor structure rather than as a purely visual, proprioceptive, or spatial structure (Goodale *et al.* 1994; Rossetti and Pisella, this volume, Chapter 4; Gallese *et al.*, this volume, Chapter 17). As described in the next section, the single neuron experiments in area 5 that followed Mountcastle focused almost exclusively on the effort to distinguish sensory from motor; perception of limb position from the command to move.

6.2.4 Body representation and movement control in area 5

Area 5 projects to and receives projections from primary motor cortex, premotor cortex, and supplementary motor cortex, among other areas (Johnson *et al.* 1996; Jones, Coulter, and Hendry 1978; Jones and Powell 1970; Strick and Kim 1978); that is, it is closely connected to the motor system. To what extent is it a sensory structure or a motor structure? As described above, Mountcastle, Lynch, Georgopoulos, Sakata, and Acuna (1975) found neurons that responded best, sometimes only, during active rather than passive movements of the arm. But do these responses represent motor commands, as Mountcastle *et al.* proposed, or are they somatosensory signals, perhaps enhanced when the monkey is paying attention to its arm? Seal, Gross, and Bioulac (1982) examined this issue in monkeys that were trained to flex or extend the elbow joint. These experimenters cut the sensory nerves from the arm, and found that about 38% of the neurons in area 5 still responded just before and during arm movements. These neurons therefore responded independently of any somatosensory stimulation; their activity was internally generated.

More recent studies have confirmed that neurons in area 5, both on the surface and in the intraparietal sulcus, are active during reaching movements (Batista, Buneo, Snyder, and Andersen 1999; Lacquaniti *et al.* 1995; Snyder *et al.* 1997). Neurons in a proposed region of the intraparietal sulcus, area PRR, may be especially active in association with reaching (Snyder *et al.* 1997). These neurons respond in anticipation of the arm movement. In a delayed reaching task, the neurons respond during the delay period after the monkey is instructed where to reach but before the 'go' signal. One speculation is that the activity of these neurons represents a motor plan. However, these experiments do not distinguish between activity that ultimately causes a movement and activity that represents an arm position predicted on the basis of motor feedback.

Kalaska, Caminiti, and Georgopoulos (1983) found that when monkeys are planning to make an arm movement, area 5 neurons begin to respond on average 60 ms after the neurons in primary motor cortex. Thus at least some of the motor-related activity in area 5 could be the result of efference copy. Though motor in origin, these signals could serve a sensory function, helping to encode body posture. Lesions to motor cortex do not abolish the motor-related activity in area 5 (Bioulac, Burbaud, and Varoqueaux 1995); but it is difficult to rule out the possibility that another motor area is sending this efference-copy signal.

The critical experiment to determine whether the activity in area 5 encodes body representation or controls movement has not yet been found, and may never be. Such a distinction between sensory and motor now appears to be too simple. Area 5 may contribute to both roles. A more meaningful question might be: How far along the sensory–motor transformation does area 5 lie? For example, how do the response properties in area 5 compare to those in primary motor cortex? Several groups have studied exactly this question.

Georgopoulos and Massey (1985) found that the neuronal selectivity for the direction of hand movement was greater in primary motor cortex than in area 5, while selectivity to the static position of the hand in space was greater in area 5 than in primary motor cortex. Kalaska and colleagues (Kalaska and Hyde 1985; Kalaska, Cohen, Prud'homme, and Hyde 1990) trained monkeys to move a handle along specific trajectories while external force loads were applied to the handle. In this way, the location and direction of hand movement were dissociated from the muscular forces that the monkey used. The results showed that selectivity to the position and trajectory of the hand through space was greater in area 5 than in primary motor cortex, while selectivity to the muscular forces applied by the arm was greater in primary motor cortex than in area 5.

In summary, the differences between area 5 and primary motor cortex are relative, not absolute. Area 5 neurons may play relatively more of a representational role, keeping track of the positions and movements of limbs, while primary motor cortex may play relatively more of a dynamic role, initiating and guiding the movements. However, these two functions overlap extensively. Not only do some area 5 neurons have motor properties, but most primary motor neurons have sensory properties, responding to tactile stimuli and joint rotation (Gentilucci *et al.* 1988). Indeed, primary motor cortex receives direct projections from almost every stage of the somatosensory system, including SI and even the somatosensory thalamus (for review, see Mountcastle 1984). The somatosensory–motor system, therefore, is organized as a set of highly interconnected nodes that collectively participate in the sensory guidance of movement. The evidence so far suggests that among these many nodes, area 5 is relatively more specialized for encoding the spatial configuration of the body.

6.2.5 Visual representation of arm position in area 5

The studies reviewed so far focused on the role of proprioception and motor control in body representation. However, other sources of information are also important in body representation. According to psychophysical studies discussed in the second half of this article, vision is sometimes the dominant sense of arm position. Does area 5 use visual input to help encode the position of the arm?

Graziano, Cooke, and Taylor (2000) examined the visual representation of arm position in monkey area 5 by manipulating two variables: (1) the position of the monkey's arm while it was out of view, under an opaque plate; (2) the position of a visible false arm, placed on top of the plate (see Fig. 6.2). The false arm was a monkey arm prepared by a taxidermist and arranged in a realistic fashion, positioned to appear as if it were extending from the shoulder of the experimental monkey. The monkey fixated on a central spot during these tests. About 25% of the neurons tested in area 5 were significantly affected by the visual position of the false arm. The proportion was significantly higher

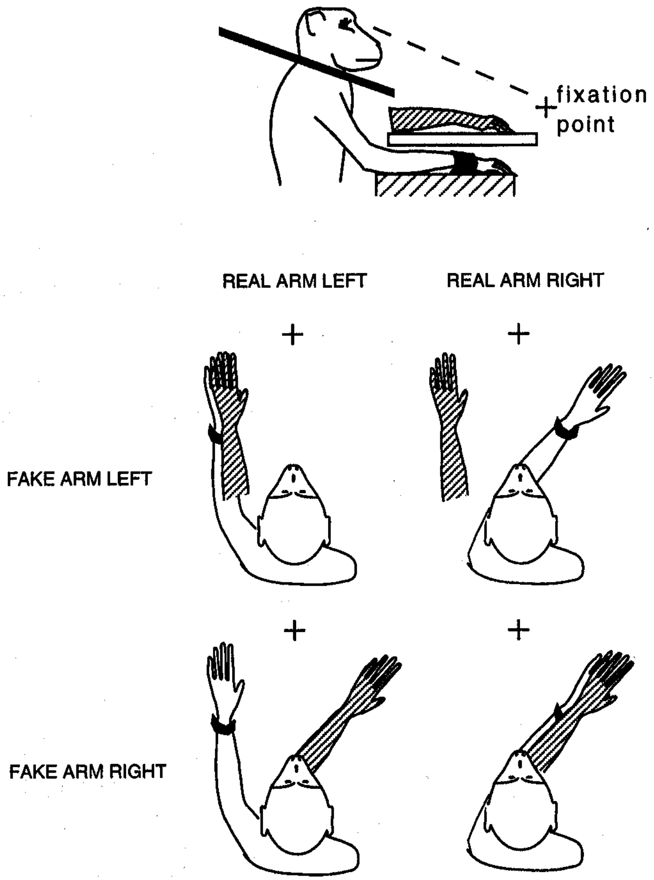


Fig. 6.2 Diagram of apparatus for testing whether neurons are sensitive to the felt or seen position of the arm. The monkey's real arm was held in an adjustable arm holder covered from view while a realistic fake arm was in view. The real arm and the visible fake arm were placed on the left or right resulting in four experimental conditions. The monkey was trained to fixate on a central light-emitting diode.

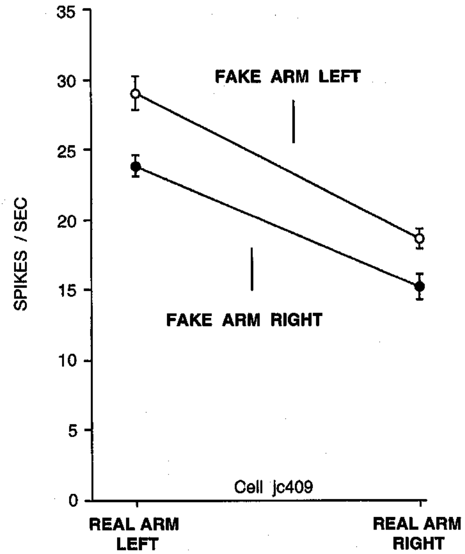


Fig. 6.3 Convergence of visual and somatosensory signals about arm position on an area 5 neuron. The neuron fired at a higher tonic rate when the monkey felt its arm to be on the left. It also fired at a higher tonic rate when the monkey saw the fake arm to be on the left. Each point is an average of 10 trials. Error bars are standard error. See Fig. 6.2 for methods.

in MIP (35%) than in 5A (18%), suggesting that there might be a hierarchy of areas in which the visual sense of arm position is more fully developed in MIP (see Fig. 6.1 for location of MIP and 5A). Data from a typical example neuron is shown in Fig. 6.3. The tonic firing rate of the neuron was significantly higher when the real arm was on the left. The firing rate was also significantly higher when the fake arm was on the left. That is, this neuron integrated the felt position of the real arm and the seen position of the false arm. This result suggests that area 5 neurons encode the position of the arm in a supramodal fashion, using both somesthesis and vision. Similar tests using objects other than a fake arm, such as a white rectangle the same approximate size as the arm, or a piece of fruit to which the monkey appeared to attend, did not affect the activity of the neurons in the same fashion.

In the same study, Graziano *et al.* (2000) found that neurons in SI were not sensitive to the seen position of the false arm. That is, in the ascending somatosensory pathway from the periphery to SI to area 5 and beyond, the first stage at which visual information about arm position is integrated with somatosensory information appears to be in area 5. This finding is consistent with the view that area 5 is a central node in representing the configuration of the body. It receives all necessary signals, including proprioception, motor feedback, and vision, and combines these signals to encode the relative positions of body parts.

Area 5 projects to many cortical regions, including premotor and motor cortex, where information about body configuration would be useful for planning movements. In the following section we describe the properties of neurons in premotor cortex that integrate the body representation with the representation of space surrounding the body. These neurons encode the locations of objects in space relative to the body, perhaps for the purpose of guiding movements.

6.2.6 Premotor cortex: a convergence of body representation, visual space, and movement control

Neurons in the caudal premotor cortex of monkeys, just posterior to the bend in the arcuate sulcus, process and encode the locations of visual, tactile, auditory, and remembered stimuli and may help to guide movements of the head and arms (Gentilucci *et al.* 1988; Graziano, Hu, and Gross 1997a,b; Graziano, Reiss, and Gross 1999). About 40% of the neurons are bimodal, responding both to tactile and to visual stimuli (Gentilucci *et al.* 1988; Graziano *et al.* 1997a; Rizzolatti *et al.* 1981). The tactile receptive fields are arranged to form a somatotopic map. The visual receptive fields are usually adjacent to the tactile ones and extend outward from the skin about 20 cm (see Fig. 6.4). The area therefore contains a somatotopically organized map of the visual space that immediately surrounds the body. For most bimodal cells, the visual receptive field is anchored to the site of the tactile receptive field on the body. When the monkey's eyes move, the visual response may change magnitude, but the location of the visual receptive field does not change (Fogassi *et al.* 1992, 1996; Gentilucci *et al.* 1983; Graziano, Yap, and Gross 1994; Graziano *et al.* 1997a). If the tactile receptive field is on the head, then rotating the head will cause the visual receptive field to move in tandem with the head (Graziano *et al.* 1997a,b). If the tactile receptive field is on the arm, moving the arm to different positions will cause the visual receptive field to move in the same direction as the arm (Graziano *et al.* 1994, 1997a). The arm-related neurons are influenced by the sight of a fake arm as well as by the felt position of the real arm (Graziano 1999). In a recent experiment mapping the precentral gyrus, these multimodal neurons were found in a relatively restricted zone in the caudal part of premotor cortex (Graziano and Gandhi 2000). Other studies on more rostral and ventral regions in premotor cortex have found neuronal properties that may be somewhat different; but because of differences in experimental technique, the studies are difficult to compare (Mushiake, Tanatsugu, and Tanji 1997).

The bimodal neurons in caudal premotor cortex bind together body representation with the visual space surrounding the body and the tactile space on the body. They encode the locations of objects in body-part centered coordinates. One possibility is that these neurons form a mechanism for guiding movements of the limbs and head away from nearby objects, for flinching and avoiding. That is,

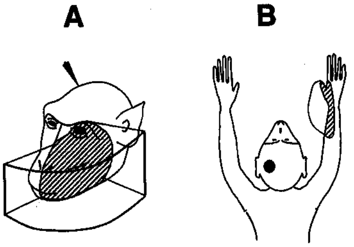


Fig. 6.4 Receptive fields of two bimodal, visual-tactile neurons in the polysensory zone in premotor cortex. (A). The tactile receptive field (shaded) is on the snout, mostly contralateral to the recording electrode (indicated by the arrowhead) but extending partially onto the ipsilateral side of the face. The visual receptive field (boxed) is contralateral and confined to a region of space within about 10 cm of the tactile receptive field. (B). The tactile receptive field for this neuron is on the hand and forearm contralateral to the recording electrode (indicated by the black dot) and the visual receptive field (outlined) surrounds the tactile receptive field. (Adapted from Graziano and Gross 1998.)

these multimodal receptive fields may form a type of protective shell around the body, alerting the brain of any potentially noxious object impinging on near space. As described in the following sections, similar interactions among vision, touch, body representation, and the control of movement can be seen in behavioral studies on humans.

6.3 The psychology of the body representation

6.3.1 The body schema

In this section, we turn from neurophysiological to psychological work on body representation. One of the most important general findings of psychological experiments is that the body representation involves more than the mere registration of peripheral inputs. Rather, it involves the interpretation of these inputs in the context of a rich internal model of the body's structure. In what follows, we refer to this internal model as the 'body schema'. While this term has been used in many different ways in past work (for discussion, see Gallagher 1986), we use the term broadly to mean an implicit knowledge structure that encodes the body's form, the constraints on how the body's parts can be configured, and the consequences of this configuration on touch, vision, and movement. The body schema plays a central role in interrelating concurrent perceptual inputs, allowing for the reconstruction of missing information, enabling the detection and resolution of conflicts, and ensuring an integrated, globally consistent, multimodal representation of the body's configuration. The body schema may even be used to interpret the seen body configuration of others (Shiffrar and Pinto, this volume, Chapter 19). In the following sections we discuss different types and combinations of information that are coordinated through the body schema.

6.3.2 Converting proprioceptive inputs into a representation of body position

The body schema is not simply a representation of joint angles, but a complex integration of vision, proprioception, touch, and motor feedback. The relative weights applied to these various sources of information probably depend on the quality of information from each source (Stark and Bridgeman 1983). In this section we discuss one source of information about body configuration; proprioception. In the subsequent sections, we will discuss the interactions between proprioception, touch, vision, and motor feedback.

Proprioception derives originally from the local forces acting on muscle spindles, joint receptors, and tendon receptors. However, behavioral data, in line with everyday experience, suggests that this raw sensory information is ultimately combined with knowledge of the body's segmental structure in order to produce a representation of the body's current spatial configuration. One indication of this transformation from simple joint information to a more complex body representation is that human subjects are more accurate at judging the spatial orientation of limb segments than they are at estimating the angles of individual joints (Soechting 1982). Another indication is the phantom limb phenomenon. Here, an amputated arm or leg continues to be experienced as present, and occupying its former location in space. This phenomenon is thought to involve continued input to areas of cortex formerly responsible for representing the position of the missing limb (for a review, see Ramachandran and Hirstein 1998). The fact that this input is translated into a detailed limb representation indicates that peripheral information is interpreted with reference to a centrally maintained model of the body's form.

In order to transform peripheral signals into a representation of posture, the brain must integrate information from different, potentially distant, parts of the body. For example, the judgement of forearm orientation requires information concerning shoulder and elbow positions, at the least. This integration is reflected in the behavior of neurons in cortical area 5, which as noted above combine information about multiple joints. The same type of integration can be seen in human behavioral studies, such as those performed by Lackner (Lackner 1988; Lackner and Taublieb 1983). Lackner took advantage of an illusion produced by vibration. If the experimenter applies vibration at about 100 Hz to a muscle or its tendon, and prevents movement resulting from the associated reflex contraction, the subject experiences the illusion of movement around the joints crossed by that muscle. For example, vibration of the biceps produces an illusion of elbow extension, and vibration of the triceps one of elbow flexion. Lackner (1988) found that under appropriate circumstances vibration of a single muscle group could produce the perception of rather global shifts in posture. For example, for subjects seated on the floor with the right hand under the right buttock, biceps vibration produced not only the illusion of arm extension, but also of a tilting of the body toward the left, as would occur if the arm really did extend and push against the floor (see also Roll, Roll, and Velay 1991). Similarly, while biceps vibration in the standing position ordinarily produces an illusion of movement only in the vibrated arm, if the subject grasps the left wrist with the right hand, vibration of the right biceps produces the illusion of movement of both arms (Craske, Kenny, and Keith 1984). These effects suggest that proprioceptive information deriving from multiple joints, tendons, and muscles is integrated into an internally consistent model of body position that takes into account the constraints imposed by the body's structure.

6.3.3 *Representing the size and shape of body parts*

In order to convert joint and muscle information into a representation of body position, the brain's model of the body must include information about the size and shape of the body's parts. The brain must also be able to update this model as body shape changes over the course of development. An experiment by Craske, Kenny, and Keith (1984) demonstrated how the perception of the body's dimensions can be recalibrated to maintain consistency with other sources of information. In this study, subjects seated in the dark extended both arms and used their right index finger to touch a position on their left arm. A mechanical device was used to produce a mismatch between the position of the right hand and the location stimulated on the left arm, such that the touch actually occurred 12.5 cm closer to the shoulder. After a period of exposure to this mismatch, subjects reported feeling that their left arm was longer than their right. That is, the representation of arm length had been updated to resolve a conflict between proprioception and touch.

Another demonstration of the same phenomenon was provided by Lackner (1988). In this experiment, each subject was asked to grasp his or her own nose, with eyes closed. Vibration was then applied to the biceps of the grasping arm. The resulting illusion of arm extension was accompanied by a feeling that the nose had become elongated. 'Oh my gosh!,' one subject exclaimed, 'My nose is a foot long! I feel like Pinocchio.'

Lackner's illusion, like the other phenomena we have described above, highlights two important aspects of the body schema. First, the body schema contains geometrical information about the hinged and segmented structure of the body, such as that extension of the arm means an increase in the distance of the hand from the face, and that the tip of the nose is connected with the rest of the face. Second, the brain will update and even distort this model of the body in order to resolve conflicts of information.

6.3.4 Body position and the interpretation of touch

One important role for body representation is to support the perception of objects in the environment surrounding the body. For example, in order to perceive the shape, location, and orientation of an object being felt with the hand, it is necessary to have an accurate representation of the hand's posture and location. This ability to integrate the sense of touch with the body representation might be related to the neurons in area 5 that have combined tactile and proprioceptive receptive fields, as discussed above.

Psychological experiments in humans have also explored the relationship between touch and body representation. For example, Driver and Grossenbacher (1996) had subjects perform a tactile discrimination task with one hand while attempting to ignore concurrent stimulation to the other hand. They found that subjects performed better when the two hands were held farther apart, indicating that attentional mechanisms were working within a spatial representation of touch that incorporated hand position.

Closely related findings come from work on patients with hemispatial neglect after parietal lobe injury. Driver, Mattingley, Rorden, and Davis (1997) studied tactile extinction, the failure to detect the more contralesional of two simultaneous touches on the body. They found that if both hands were touched, the patients showed greater tactile extinction when the two hands were held close together than when they were held far apart. Aglioti, Smania, and Peru (1999) found that for some neglect patients, if the two hands were crossed, such that the left hand was to the right of the trunk and the right hand to the left of the trunk, the tactile neglect switched hands, to remain on the contralesional side of the trunk. In a related study, Moscovitch and Behrmann (1994) asked patients to hold out one hand with the palm up. When both sides of the wrist were touched, the patients neglected the touch on the contralesional side. The patients were then asked to turn the hand so that the palm faced down. Under this condition, the patients neglected a touch on the opposite side of the wrist, that is, still toward the contralateral side of the body.

The integration of touch with body position information is especially important for stereognosis, the use of touch to judge the size and shape of objects. Illusions in stereognosis can occur when body position is misperceived. One such illusion, described originally more than two thousand years ago by Aristotle (described in Benedetti 1985), is caused by holding a small ball between the crossed third and fourth fingers. This situation produces the perception that the ball has doubled, and that two separate objects are contacting the fingertips. Benedetti (1985, 1988) in somewhat more recent studies of this phenomenon showed that the doubling occurs because the tactile input is interpreted as if the fingers were uncrossed. This 'tactile diplopia' that occurs when objects are explored with the hand in a highly unfamiliar posture disappears if the subject is given extended experience with that hand position (Benedetti 1991). This result may be related to the reorganization in somatosensory cortex that occurs after practice with a particular task (Jenkins *et al.* 1990) and after changes in hand structure, for example after surgically induced syndactyly (Allard, Clark, Jenkins, and Merzenich 1991).

6.3.5 Coordinating seen and felt body position

Just as the body schema links touch and proprioceptive information, it also links proprioception with vision and oculomotor function. One demonstration of this connection is that subjects can fixate the position of their fingertip in the dark, and moreover can track its motion with smooth pursuit eye movements (Jordan 1970). Furthermore, illusions of arm movement can produce illusions of visual motion; if a diode is affixed to the fingertip, and an illusion of arm flexion is induced by muscle vibration, the light appears to move in the direction of the perceived arm movement (DiZio, Lathan, and Lackner 1993). Conversely, visual inputs can influence proprioception, as demonstrated by the phenomenon of visual capture. Here, viewing one's hand through a prism results in a distortion of proprioceptive perception such that the hand is felt to lie in the location where it is seen (Hay, Pick, and Ikeda 1965; Welch 1986). Another version of visual capture occurs in patients with phantom limbs. If these patients view the intact arm in a mirror, such that its reflected image appears in the location formerly occupied by the missing limb, then movement of the intact arm can induce the perception of identical movements in the phantom (Ramachandran and Hirstein 1998).

After prolonged exposure to a visual-proprioceptive mismatch, the mechanisms serving to coordinate the two modalities can themselves be altered. This adaptation is shown by many experiments with prism-induced visual displacements (Redding and Wallace 1997; Welch 1986). When pointing to targets viewed through a laterally displacing prism, subjects initially misreach in the direction of the visual displacement. However, after continued exposure to the prism, reaching becomes more accurate. After such adaptation, if the prism is removed and the subject is asked to reach for targets viewed normally, misreaching tends to occur in the direction opposite to the previous visual displacement. If a prism-adapted subject is asked to close his or her eyes and position the adapted hand so that it feels straight ahead of the nose, the subject will misplace the hand off the body midline, suggesting that adaptation to the initial visual–proprioceptive mismatch has led to a recalibration of the felt position of the arm (Harris 1965).

6.3.6 Interrelating multiple perceptual modalities

A number of studies indicate that the body schema can coordinate even rather complex relationships among sensory modalities, including three-way interactions among touch, vision, and proprioception. For example, directing the eyes toward a particular part of the body, even in the dark, enhances the tactile sensitivity of that part (Tipper *et al.* 1998). Another demonstration of such three-way coordination was provided by Driver and Spence (1998). They found that a brief touch on the hand enhanced the subsequent processing of visual stimuli near the hand. The touch seemed to draw visual attention to the region of space near the hand. This enhanced visual region was anchored to the hand and moved to different locations in space when the hand was moved, even when the hands were crossed. Likewise, a flash of light presented near the hand enhanced the subsequent processing of tactile stimuli applied to the hand. In both versions of the experiment, crossmodal attention between vision and touch was operating on representations that had already taken body configuration into account.

Crossmodal attention has also been studied in patients with brain injury. Di Pellegrino, Ladavas, and Farne (1997) reported on a patient with right fronto-temporal damage and symptoms of tactile extinction. This subject was asked to detect a tactile stimulus applied to the contralesional hand. When a visual stimulus was simultaneously presented near the ipsilesional hand, the subject no longer reported the tactile stimulus. That is, the tactile stimulus had been extinguished by the competing visual stimulus. The critical region of visual space, in which the competing stimulus was most effective, surrounded the ipsilesional hand and moved if the hand was moved. That is, touch, vision, and proprioception were bound together in a framework provided by the body schema. A similar close association between vision, touch, and proprioception occurs in the bimodal visuotactile neurons in premotor cortex, discussed above, an area that may have been damaged in the patient considered in the di Pellegrino study.

An experiment by Botvinick and Cohen (1998) showed that perceptual information can sometimes be distorted in order to maintain consistency in the three-way relationship among vision, touch, and proprioception. This study reported a novel illusion, produced by introducing a spatial mismatch between seen and felt touch. The effect was elicited in the following manner (see Fig. 6.5): a rubber replica of a human hand was placed on a table in front of the subject. The subject's own hand was positioned out of view, behind a screen. As the subject watched the rubber hand, the experimenter stroked it with a brush and, at the same time, brushed the subject's own hand in an identical manner. Subjects reported a spatial fusion between the seen and felt touch, as if they were feeling the touch of the brush in the location where they saw the rubber hand touched. They often described this illusion by saying that it felt as if the rubber hand had become 'their' hand (see Fig. 6.6).

The rubber hand illusion provides another example of the body schema mediating in the resolution of a conflict; the perception of felt touch was brought into spatial alignment with the visually perceived touch, much as a ventriloquist's voice is aligned with his dummy's moving mouth. Botvinick and Cohen (1998) reasoned that this realignment of visual and tactile representations should involve a distortion of proprioceptive information, causing the subject's arm to be represented in a position that would place his hand in the position of the rubber hand. They predicted that if proprioceptive information was indeed being distorted in this way, then prolonged exposure to the illusion should give rise to effects on reaching similar to those observed in prism adaptation experiments. Indeed, the subjects did show a reaching bias consistent with a recalibration of proprioception. Furthermore, the magnitude of the reaching bias correlated positively with the reported duration of the illusion.

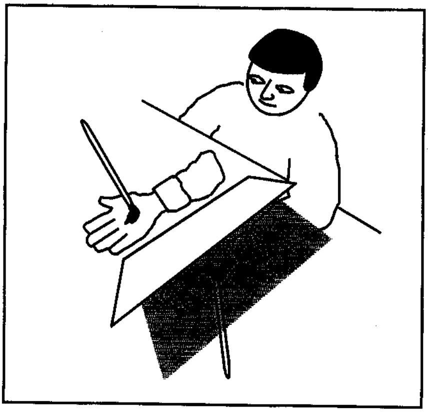
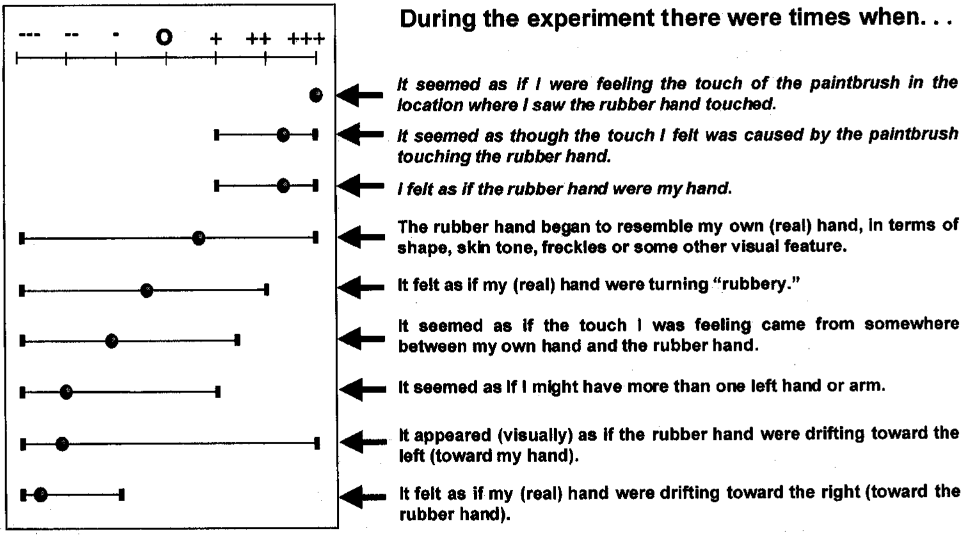


Fig. 6.5 Arrangement used in eliciting the rubber hand illusion. The subject's hand, out of view, was stroked with a paint brush while a rubber hand, in view, was synchronously stroked.



During the experiment there were times when...

It seemed as if I were feeling the touch of the paintbrush in the location where I saw the rubber hand touched.

It seemed as though the touch I felt was caused by the paintbrush touching the rubber hand.

I felt as if the rubber hand were my hand.

The rubber hand began to resemble my own (real) hand, in terms of shape, skin tone, freckles or some other visual feature.

It felt as if my (real) hand were turning "rubbery."

It seemed as if the touch I was feeling came from somewhere between my own hand and the rubber hand.

It seemed as if I might have more than one left hand or arm.

It appeared (visually) as if the rubber hand were drifting toward the left (toward my hand).

It felt as if my (real) hand were drifting toward the right (toward the rubber hand).

Fig. 6.6 Questionnaire results from Botvinick and Cohen (1998). Subjects were asked to rate the accuracy of each statement on a seven-point scale ranging from 'disagree strongly' (---), through 'neither agree nor disagree' (0), to 'agree strongly' (+++). Each point is the mean rating of 10 subjects. Error bars show response range.

6.3.7 The body in action: representing the relation of target and effector

As reviewed above, neurophysiological findings in the monkey indicate that the brain does not draw a sharp boundary between its representation of the body and its representation of movement. Behavioral studies in humans point to the same conclusion. Movements appear to be planned in spatial coordinate frames that are referenced to the different parts of the body. In particular, the act of reaching toward a target is closely related to the sense of arm position.

When we reach toward a target, we normally have proprioceptive feedback from the arm, a continuous view of both the hand and the target. A number of experiments have investigated the effect of removing one or another of these sources of information. For example, vision of the hand throughout the reach improves accuracy (Desmurget *et al.* 1995; Prablanc *et al.* 1979). The importance of the view of the hand is especially clear in patients who have lost proprioceptive sense in their arms due to nerve degeneration. These patients have no other sense of arm position than vision. If these patients reach toward a target without the sight of their hands, they make large errors in both direction and extent (Ghez *et al.* 1995). Vision of the hand can influence not only the accuracy of pointing, but also the path used to reach the target. Wolpert, Ghahramani, and Jordan (1995) showed that if the hand trajectory as seen by the subject is distorted by increasing its curvature, subjects adapt by reaching along paths curved in the opposite direction, apparently seeking to produce reaches that follow a straight line in visual space. Vision of the hand can affect reaching performance even if the hand is viewed only prior to reach initiation. A glimpse of the hand in its resting position prior to movement has been shown in a number of studies to improve reach accuracy (Desmurget *et al.* 1997; Prablanc *et al.* 1979). Furthermore, if the subject wears a displacing prism and is given a brief initial view of the hand, the subsequent reach is misdirected, indicating again that the position of the hand, in this case mislocalized by the subject, is incorporated into the motor program (Rossetti, Desmurget, and Prablanc 1995).

Collectively, these studies show that the location of the hand is continuously monitored and used during reaching. One hypothesis is that the brain computes the current location of the target relative to the hand, and then uses this hand-centered spatial information to guide the movement of the hand (Graziano and Gross 1998). Several studies have found that the errors in reaching to a visual or remembered target tend to be along the line between the starting position of the hand and the target (Chieffi *et al.* 1999; Gordon *et al.* 1994; Soechting and Flanders 1989). This result suggests that the visuomotor system does indeed compute the distance and direction of the target from the hand, with greater error in the computation of distance. McIntyre *et al.* (1998) found that the pattern of errors during reaching supported both an eye-centered and a hand-centered reference frame. They point out that their findings are consistent with a final transformation into a hand-centered frame.

Tipper, Lortie, and Baylis (1992) found evidence that attention to visual stimuli during a reaching task may be linked to the position of the hand. In their study, subjects reached for a target while avoiding a distracting stimulus. The reaction times were longer when the distracter lay roughly between the hand and the target. The critical region of visual space, in which the distracter had maximum effect, was anchored to the hand and moved if the hand was placed in different starting locations. In several conceptually related experiments (Anzola, Bertoloni, Buchtel, and Rizzolatti 1977; Wallace 1971), subjects pressed a button in response to a flashed light. If the flash of light was in the space near the hand, the subjects responded more quickly. For example, when subjects were asked to respond to a light on the right side of visual space by pressing a button with the left hand, and to a light on the left side using the right hand, they were faster when the hands were crossed than when they were uncrossed.

In summary, there is accumulating behavioral evidence that during movement of the arm and hand, stimuli are encoded in a spatial reference frame that is anchored to the hand, at least at some point during the movement planning. This result matches the findings in monkey premotor cortex. As described above, some of the multimodal neurons in premotor cortex that are related to arm movement also have visual receptive fields that are anchored to the arm and hand, apparently encoding the locations of nearby objects in arm- and hand-centered coordinates. The behavioral results suggest that humans may also have hand-centered visual receptive fields. This type of spatial coding, in body-part centered coordinates, would bind together the representation of the body and of the visual space around the body with the control of movement.

6.3.8 Development of the body schema: the roles of nature and nurture

As the body changes size and shape over the life-span, the internal model of the body must change accordingly. A wealth of experimental and clinical data, some of which we have already reviewed, shows just how plastic the body schema can be, even in adulthood. A classic example of this adaptation is the phenomenon of prism adaptation, discussed above. The body schema can also be modified by injuries that deform the limbs. In cases where the deformed limb is amputated, the patient often reports experiencing a phantom limb with the same deformity (Ramachandran and Hirstein 1998).

While experience seems certain to play an important role in the construction and continual modification of the body schema, at least some elements of the body schema may not depend on experience, or at least may be present very early in life (Bahrick and Watson 1985). Rochat and colleagues (Morgan and Rochat 1997; Rochat 1998) investigated the development of the body schema in infancy, and found that infants as young as three months were able to match proprioceptive events to visual ones. Other researchers found evidence of visual–proprioceptive matching even shortly after birth (Meltzoff and Moore 1983). One of the most compelling arguments for an innate body schema is the phenomenon of the aplastic phantom. Here, a person congenitally lacking a limb experiences a full-fledged phantom in place of the missing limb (Saadah and Melzack 1994). While findings such as these are intriguing, the relative roles of nature and nurture in establishing and calibrating the body schema remain poorly understood, and present an important area for future research.

In investigating how the body schema emerges during infancy, some developmental psychologists have also asked the question of how the body comes to be distinguished from other objects as belonging to the self. Rochat (1998) suggested that the detection of correlations among visual, proprioceptive, tactile, and motor signals provides the basis for the identification of the body as self. It is interesting that focal brain lesions, especially to the right parietal lobe, can cause the denial of ownership of intact body parts (Kolb and Whishaw 1990); perhaps the loss of the sense of self in these patients is due to a disruption of Rochat's crossmodal mappings.

6.4 Conclusions

We have described neurophysiological work in monkeys and psychological work in normal and brain-damaged humans on the internal representation of the body. Between these different approaches, an enormous amount is now known about the body representation. The critical brain areas have been identified; they include area 5 in the superior parietal lobe, and possibly other areas such as premotor and motor cortex. A main finding of both the neurophysiological and the psychological approach is that the body representation is not merely a simple code for joint angles. Instead, proprioceptive information is combined with visual, tactile, and motor-feedback signals. All of this information is interpreted in the context of an internal model of the geometry of the body. The body schema appears to be a device for cross-referencing between sensory modalities, and for guiding movement of the limbs through space.

Just as the body schema itself lies at the crossroads of multiple sensory modalities and in the communication among multiple cortical regions, its study traverses multiple disciplines. Progress in understanding the body schema will come from the continued, rich interrelations between psychophysics, neuropsychology, and neuroscience.

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