# Part II

# Neural processes

# 9 A map of complex movements in motor cortex of primates

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## Abstract

We used electrical microstimulation to study the organization of motor cortex in awake monkeys. Stimulation on a behaviourally relevant time scale (0.5–1 s) evoked coordinated, complex postures that involved many joints. For example, stimulation of one site caused the mouth to open and also caused the hand to shape into a grip posture and move to the mouth. Stimulation of this site always drove the joints towards this final posture, regardless of the initial posture. Stimulation of other cortical sites evoked different postures. Postures that involved the arm were arranged across cortex to form a map of hand positions around the body. This map encompassed both primary motor and lateral premotor cortex. Primary motor cortex appears to represent the central part of the workspace, where monkeys most often manipulate objects with their fingers. These findings suggest that primary motor and lateral premotor cortex might not be arranged in a hierarchy, but instead might operate in parallel, serving different parts of the workspace.

## Introduction

How does the primate cerebral cortex control movement? Over the past century, three interrelated hypotheses have shaped the research. They are now thought to be at least partly incorrect. They are:

1 Primary motor cortex contains a detailed topographic map of the body. The foot is represented at the top of the hemisphere, the mouth is represented at the bottom, and other body parts are systematically arranged in between.
2 Each point in the map specifies the tension in a muscle or small group of related muscles. The pattern of activity across the map thus specifies a pattern of muscle tensions across the body.
3 The cortical motor areas are hierarchically organized. Premotor cortex projects to and controls primary motor cortex, which projects to and controls the spinal cord.

These three hypotheses were summarized as long ago as 1938 by Fulton. Since then a growing body of evidence has cast some doubt on them.

1 Investigators failed to find the hypothesized orderly map of the body in primary motor cortex (Sanes & Schieber, 2001). The somatotopy is fractured and intermingled (Donoghue, LeiBovic, & Sanes, 1992; Gould, Cusick, Pons, & Kaas, 1986; Nudo, Jenkins, Merzenich, Prejean, & Grenda, 1992; Penfield & Boldrey, 1937; Sanes, Donoghue, Thangaraj, Edelman, & Warach, 1995; Schieber & Hibbard, 1993; Woolsey, Settlage, Meyer, Sencer, Hamuy, & Travis, 1952). A broad organization exists, with a medial hind limb region, a lateral face region and a forelimb region in between. These regions partly overlap. The extent of somatotopy within each region is in debate. In the forelimb region, the fingers are represented in an intermingled fashion and overlap at least partly with a representation of the arm (Donoghue et al., 1992; Park, Belhaj-Saif, Gordon, & Cheney, 2001; Schieber & Hibbard, 1993).

2 It is now understood that each site in cortex does not control one muscle. The connectivity is more complex. Some investigators suggest that neurons in motor cortex influence high-level aspects of movement, such as direction or velocity of the hand through space (Caminiti, Johnson, & Urbano, 1990; Georgopoulos, Lurito, Petrides, Schwartz, & Massey, 1989; Georgopoulos, Schwartz, & Kettner, 1986; Reina, Moran, & Schwartz, 2001). Others suggest that joint angle is coded in motor cortex (Scott & Kalaska, 1995, 1997) or that muscle tension is coded, perhaps in a complex fashion in which each location in cortex influences many muscles (Cabel, Cisek, & Scott, 2001; Donoghue et al., 1992; Evarts, 1968; Kakei, Haffman, & Strick, 1999; Todorov, 2000). Some suggest that several of these movement parameters are simultaneously encoded by motor cortex neurons (Kakei et al., 1999). The debate has not yet been resolved. Indeed, almost every movement parameter that has been tested has been found to be correlated with the activity of motor cortex neurons.

3 The hierarchical organization among the cortical motor areas is in question. Since Fulton (1938), many new motor areas have been described, including the supplementary and cingulate motor areas (He, Dum, & Strick, 1995; Penfield & Welch, 1949; Woolsey et al., 1952) and many subdivisions of premotor cortex (e.g. Rizzolatti and Luppino, 2001; Wise, Boussaoud, Johnson, & Caminiti, 1997). The hierarchical relationship among these areas is not certain, because many of them project to the spinal cord in complex, overlapping patterns (e.g. Dum & Strick, 1991, 1996; Maier, Armond, Kirkwood, Yang, Davis, & Lemon, 2002; Murray & Coulter, 1981). Lesions to the traditional "primary" motor cortex result in a specific deficit in complex finger coordination rather than a general deficit in movement

(e.g. DennyBrown & Botterell, 1947; Kermadi, Liu, Tempini, Wiesendanger, & Rouiller, 1997; Rouiller, Yu, Moret, Tempini, Wiesendanger, & Liang, 1998; Travis, 1955).

To address some of these unresolved questions, we recently electrically microstimulated sites in motor cortex of monkeys (Graziano, Taylor, & Moore, 2002). Each site was stimulated for 500 ms, matching the time scale of a monkey's natural arm and hand movements (e.g. Georgopoulos et al., 1986; Reina et al., 2001). This stimulation caused the monkey to enact complex, coordinated movements such as reaching, grasping or pantomiming a flinch from a nearby object. The evoked movements were arranged across the cortical surface in a rough map of spatial locations to which the movements were directed. The map included parts of both primary motor and premotor cortex. Primary motor cortex emphasized hand locations in central space and manipulatory postures of the fingers and wrist. Premotor cortex emphasized other regions of space, such as grip postures near the mouth or reaching postures in lateral space.

Our stimulation results are consistent with previous findings; that is, we found a rough somatotopic organization of body parts though not muscles, and systematic differences between the traditional primary motor and premotor areas. However, our results suggest a modification of the traditional hypotheses described above. The results raise the possibility that motor cortex controls movement by means of a map of complex, behaviourally meaningful actions; and that primary and premotor cortex may be different because they encode different types of actions in different parts of space. Our aim here is to evaluate these possibilities in light of previous findings on motor cortex.

## The use of electrical stimulation to study brain function

Electrical stimulation of motor cortex dates back to Fritsch and Hitzig (1870), who used stimulating electrodes on the surface of the dog brain to demonstrate a rough somatotopic organization. Over the next 80 years, many experiments obtained similar results in monkeys, apes and humans (e.g. Ferrier, 1873; Foerster, 1936; Fulton, 1938; Penfield & Boldrey, 1937; Sanes & Schieber, 2001; Woolsey et al., 1952).

Asanuma and colleagues pioneered the use of low currents delivered through a microelectrode (e.g. Asanuma, 1975; Asanuma & Arnold, 1975; Asanuma, Arnold, & Zarzecki, 1976; Stoney, Thompson, & Asanuma, 1968). This technique was subsequently used by many others (e.g. Huntley & Jones, 1991; Kurata, 1989; Sato & Tanji, 1989; Sessle & Wisendanger, 1982; Stepniewska, Preuss, & Kaas, 1993; Strick & Preston, 1978; Weinrich & Wise, 1982; Wu, Bichot, & Kaas, 2000). Most of these experiments used brief trains of electrical pulses, each train typically less than 20 ms, to evoke a muscle twitch. The purpose of these previous studies was to map the location on the body affected by stimulation, rather than to study the evoked movement itself.

Microstimulation has now become widely used to study the function of many brain areas outside of motor cortex. When applied on a behaviourally relevant time scale, stimulation can evoke complex effects that appear to mimic the function of the directly stimulated tissue. For example, Newsome and colleagues (Salzman, Britten, & Newsome, 1990) stimulated monkey visual area MT and influenced the monkey's perceptual decisions about the motion of visual stimuli. Romo, Hernandez, Zainos, and Salinas (1998) stimulated primary somatosensory cortex and influenced the monkey's perceptual decisions about tactile stimuli. Electrical stimulation has been used to reveal functional maps of eye and head movement (e.g. Bruce, Goldberg, Bushnell, & Stanton, 1995; Freedman, Stanford, & Sparks, 1996; Gottlieb, Bruce, & MacAvoy, 1993; Robinson, 1972; Robinson & Fucjs, 1969; Schiller & Stryker, 1972; Tehovnik & Lee, 1993; Their & Andersen, 1998). Complex sexual behaviour and feeding behaviour can be elicited by stimulation of portions of the hypothalamus (Caggiula & Hoebel, 1966; Hoebel, 1969; Okada, Aou, Takaki, Oomura, & Hori, 1991; Quaade, Vaernet, Larsson, 1974).

In these studies using electrical stimulation to probe the function of a brain area, stimulation activates not only the neuronal elements near the electrode tip, but also a network of neurons sharing connections with those directly stimulated. Thus, the effect of electrical stimulation is thought to depend on a spread of signal through physiologically relevant brain circuits.

It is important to note that electrical stimulation is non-physiological and thus should always be interpreted with caution. It can presumably activate neurons in unnatural patterns. The technique is most convincing when the evoked behaviours resemble naturally occurring behaviours, are organized in the brain in an orderly functional architecture, and match other known properties of the brain area such as single neuron properties and the effects of lesions.

As described in the next section, we stimulated motor and premotor cortex for 500 ms, on the same time scale as the reaching movements that monkeys typically make, and also on the same time scale as the elevated activity of motor cortex neurons during reaching (e.g. Georgopoulos et al., 1986; Reina et al., 2001). This duration of stimulation is within the range of the studies cited above, and the current intensities that we used are within the range used in the oculomotor studies.

## A map of complex postures evoked by microstimulation in motor cortex

In this section, we first describe the results of stimulation on a behavioural time scale of several example sites in motor cortex. Then we summarize the two main findings.

On stimulation of one site (Figure 9.1A), the contralateral hand closed into a typical precision grip posture for a monkey, with the fingers together and slightly curled and the tip of the thumb against the side of the forefinger. The wrist and forearm rotated such that the point of the grip faced the mouth. The elbow and shoulder rotated such that the hand moved smoothly to the mouth, in a manner and with a velocity profile that matched the monkey's normal hand-to-mouth movements. The mouth opened. All of these movements occurred simultaneously. The hand moved to the mouth regardless of its starting position. Once the hand reached the space in front of the mouth, it stayed at that location; the hand, arm and mouth remained in this final posture until the end of the stimulation train. The movement was repeatable and consistent across hundreds of trials and occurred even after the monkey was anaesthetized.

Stimulation of another site (Figure 9.1B) caused the contralateral elbow and shoulder to rotate such that the hand moved to a position about 10 cm in front of the chest. The hand opened into a splayed posture with the fingers straight and separated from each other. The forearm supinated such that the open palm was aimed towards the monkey's face. For this site as for the last

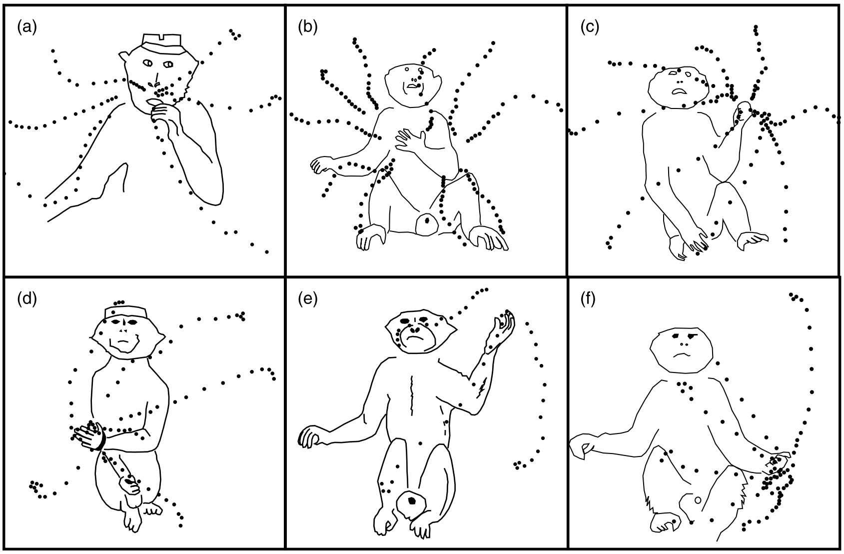

*Figure 9.1* Six examples of complex postures evoked by stimulation of the precentral gyrus. Stimulation of each cortical site in the right hemisphere evoked a different final posture of the left hand and arm. Drawings were traced from video footage taped at 30 frames per second. The dotted lines show the frame-by-frame position of the hand during stimulation. Regardless of the starting position, stimulation caused the hand to move towards a specific final position. Adapted from Graziano et al. (2002).

site, stimulation evoked the same final posture regardless of the direction of motion required to reach the posture.

Stimulation of other cortical sites evoked other complex movements (e.g. Figure 9.2C–F). These movements had two basic properties:

1. Stimulation drove the relevant joints towards a final posture, regardless of the starting posture. The joints then remained in that final posture until the stimulation train ended. Thus we did not evoke sequences of movements or repetitive movements. We did not evoke a specific direction of movement; opposing directions could be obtained depending on the starting position.
2. Sites that involved movement of the arm were arranged across the precentral gyrus to form a rough map of evoked hand position (Figure 9.2). Hand position, however, was not the only variable specified by stimulation of this map. The posture of the entire arm and sometimes of the wrist and fingers was specified. The acceleration and speed of movement to the final posture also varied among sites. Because many muscles and joints contribute to such movement towards a complex posture, the map of postures may help to explain the long-standing puzzle that different muscles and joints are represented in an intermingled fashion in motor cortex (Sanes & Schieber, 2001).

## Movement variables controlled by motor cortex

Georgopoulos et al. (1986) trained monkeys to reach in various directions from a central starting position and found that neurons in motor cortex responded during the reach. Each neuron generally responded most during one direction of reach and responded less well during neighbouring directions. That is, the neurons were tuned to the direction of reach. Although each neuron was broadly tuned, the authors pointed out that a population of such neurons could collectively provide precise spatial information about the direction of reach.

Other experiments by Georgopoulos, Ashe, Smyrnis, and Taira (1992) suggested that the code for movement in motor cortex must be more complex than a simple direction code. Many groups have since demonstrated that the firing of motor cortex neurons is correlated with parameters such as the angles of joints, the force applied by the arm muscles, and the velocity of the hand movement in space (Cabel et al., 2001; Caminiti et al., 1990; Kakei et al., 1999; Kalaska, Cohen, Hyde, & Prud'homme, 1989; Reina et al., 2001; Scott & Kalaska, 1995, 1997).

Scott and Kalaska (1995, 1997) showed that the directional preference of most neurons changed when the monkey was required to maintain a different arm posture, with the elbow raised. Thus the neurons seemed sensitive to the posture of the entire arm and how that posture changed over time, rather than reflecting only the changing position of the hand in space. Scott and

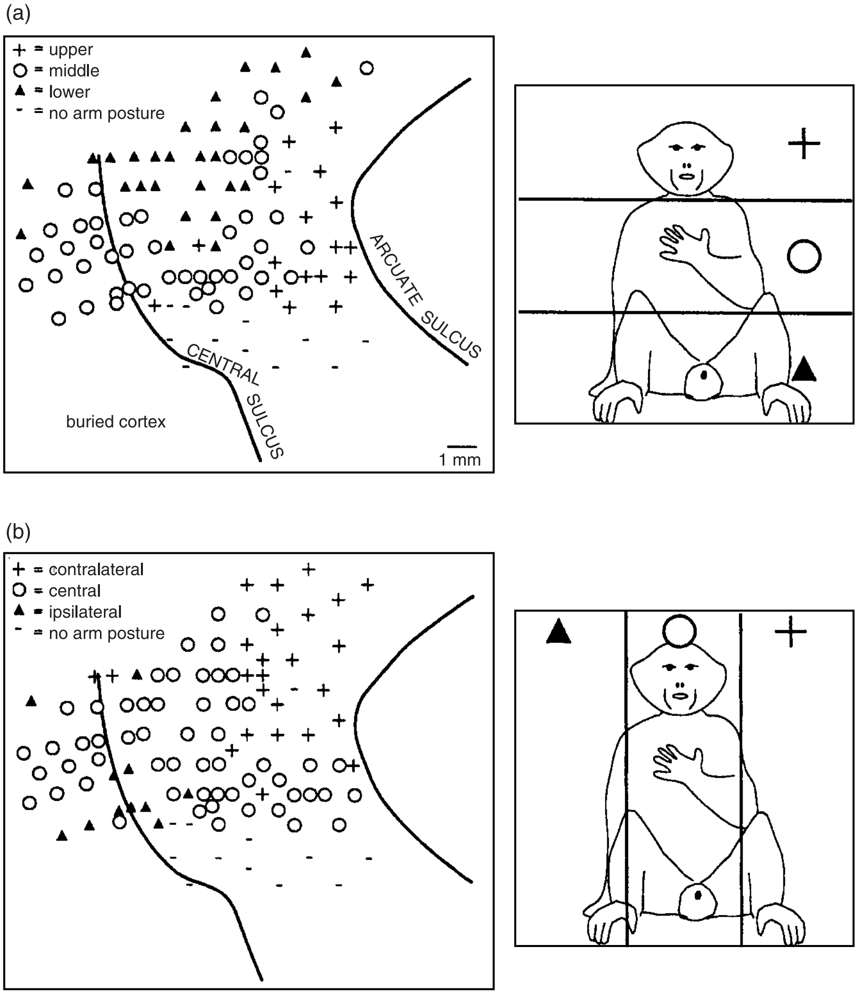

*Figure 9.2* Topography of hand and arm postures in the precentral gyrus, based on 201 stimulation sites. Sites plotted to the left of the central sulcus were located in the anterior bank of the sulcus. (a) Distribution of hand positions along the vertical axis, in upper, middle and lower space. Each site was categorized based on the centre of the range of evoked final positions. Height categories were defined as follows: lower = 0–12 cm from bottom of monkey, middle = 12–24 cm, upper = 24–36 cm. Dashes show electrode penetrations where no arm postures were found; usually the postures from these locations involved the mouth or face. (b) Distribution of hand positions along the horizontal axis, in contralateral, central or ipsilateral space. Horizontal categories were defined as follows: contralateral = 6–18 cm contralateral to midline, central = within 6 cm of midline (central 12 cm of space), ipsilateral = 6–18 cm ipsilateral to midline. Adapted from Graziano et al. (2002).

colleagues speculated that motor cortex neurons may control so-called intrinsic variables, such as muscle force and joint angle, rather than extrinsic variables, such as the position or movement of the hand in external space. Other experiments (Kakei et al., 1999) suggest that, in the case of wrist movements, the firing of motor cortex neurons is correlated with both intrinsic and extrinsic variables.

These single-neuron experiments have the limitation that they test the correlation between neuronal activity and a restricted set of simple movements. Neurons that encode complex movements might produce a confusing and diverse pattern of results when filtered through these simpler tasks. Electrical stimulation can help to resolve this difficulty, because it is a causal technique rather than a correlational one. It is possible to measure the movement that is caused by activity at a location in motor cortex.

Does electrical stimulation of motor cortex specify hand location in space, individual joint angles, or the muscle forces involved in producing a particular velocity profile? Our results suggest that all of these aspects of movement may be specified. Stimulation of each site within the arm and hand representation evoked a movement to a specific, final posture. Because the arm posture was specified, the location to which the hand moved was also specified. However, each site did not appear to encode only hand location, independent of the joint angles that composed the arm posture. There are many postures of the arm that can correspond to the same hand location, and stimulation of one site specified only one arm posture. Thus our results agree closely with the findings of Scott and Kalaska (1995, 1997) in that the posture of the arm, not merely the position or movement of the hand, appears to be of critical importance.

Dynamic aspects of movement such as the acceleration of the hand also appeared to depend on the cortical site that was stimulated. For example, for a hand-to-mouth movement, the velocity profile of the hand was appropriate for putting food in the mouth without damaging the face (e.g. 20 cm/s at peak speed for one stimulation site). For a movement in which the hand moved to an upper lateral position and turned outward as if to block an impending threat to the head, the velocity was appropriately fast, consistent with a defensive gesture (230 cm/s at peak speed for one stimulation site).

These stimulation results suggest that movement control in motor cortex might be organized in terms of behaviourally useful actions aimed towards a goal posture. In this case, asking whether the control is extrinsic, intrinsic, kinematic or dynamic may be the wrong question, or at least a question with a complex answer. Movement control in motor cortex may involve all of these aspects of movement processing, perhaps to differing degrees for different types of movement.

## Relationship between primary motor and premotor cortex

The map of stimulation-evoked arm postures that we obtained encompassed the forelimb representation in primary motor cortex, and also premotor cortex including ventral premotor (F4 and F5) and dorsal premotor (probably mainly PMDc). These areas appeared to be part of a complete, unitary map of the position of the hand in space. How can a single map be reconciled with the mosaic of separate areas described within this region of cortex?

The map of postures appeared to contain specialized subregions with different functions (Figure 9.3). One subregion corresponded to hand locations at the mouth (circles in Figure 9.3). Stimulation within this region always caused the hand to shape into a grip posture. At most hand-to-mouth sites, stimulation also caused the mouth to open. Rizzolatti and colleagues (Fogassi, Gallese, Buccino, Craighero, Fadiga, & Rizzolatti, 2001; Murata, Fadiga, Fogassi, Gallese, Raos, & Rizzolatti, 1997; Rizzolatti, Camarda, Fogassi, Gentilucci, Luppino, & Matelli, 1988) recorded from single neurons in this area, which they termed F5, and found that the neurons responded selectively during grip postures of the hand and movements of the mouth. Neurons in F5 were also active during movements of the arm, especially towards the mouth.

A second functionally distinct subregion of the map corresponded to hand locations in the space in front of the chest (triangles in Figure 9.3).

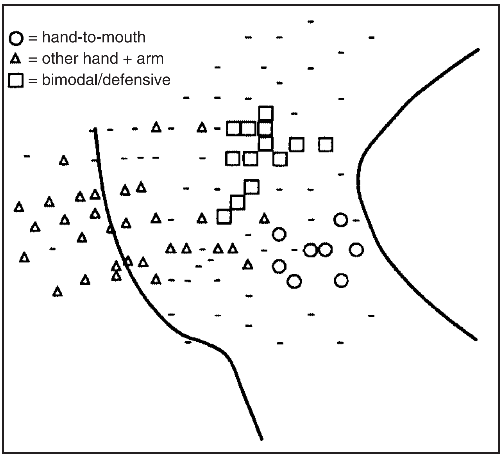

*Figure 9.3* Specialized subregions within the map of stimulation-evoked postures. Circles show hand-to-mouth sites; these always involved a grip posture of the hand in addition to a movement of the arm that brought the hand to the mouth. Triangles show other sites where stimulation evoked both a hand and an arm posture; these sites often involved the hand moving into central space and the fingers shaping into a specific configuration. Squares show sites where bimodal, visual–tactile responses were found and stimulation evoked defensive movements. Adapted from Graziano et al. (2002).

Stimulation within this part of the map evoked a variety of hand postures, including a grip with the thumb against the forefinger, a fist, an open hand with all digits splayed, rotations of the wrist, and pronation or supination of the forearm, matching the natural behaviour of monkeys during manipulation of objects within central space. This part of cortex corresponded to the primary motor forelimb representation, an area that has long been known to emphasize the control of fine movements of the fingers. Lesions to it cause a deficit in manual dexterity (e.g. DennyBrown & Botterell, 1947; Kermadi et al., 1997; Rouiller et al., 1998; Travis, 1955). The direct projections from primary motor cortex to the spinal motor neurons tend to be related to the muscles of the hand and wrist (Bortoff & Strick, 1993; Lawrence, 1994; Lemon, Baker, Davis, Kirkwood, Maier, & Yang, 1998; Maier, Olivier, Baker, Kirkwood, Morris, & Lemon, 1997). The lowest electrical thresholds in motor cortex are correlated with movements of the hand and wrist (Asanuma et al., 1976; Gentilucci, Fogassi, Luppino, Matelli, Camarda, & Rizzolatti, 1988). Neurons in primary motor cortex, especially in the posterior part, respond during movements of the fingers, and have small tactile receptive fields on the fingers (Gentilucci et al., 1988; Lemon & Porter, 1976; Wong, Kwan, MacKay, & Murphy, 1978). On the basis of our data, we suggest that the emphasis on manual dexterity may be paired with an emphasis on hand locations in central space, the monkey's "manual fovea" in which manipulation is most commonly performed.

A third subregion of the map (squares in Figure 9.3) contained neurons that responded to tactile stimuli on the face and arms, and visual stimuli near the face and arms. Stimulation of these sites evoked apparent defensive movements. This multimodal subregion is described in greater detail in the next section. It matches a part of premotor cortex where bimodal, tactile–visual neurons have been reported previously (Fogassi, Gallese, Fadiga, Luppino, Matelli, & Rizzolatti, 1996; Graziano & Gandhi, 2000; Graziano, Hu, & Gross, 1997; Graziano, Reiss, & Gross, 1999; Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981).

The single map that we obtained with electrical stimulation, therefore, may be consistent with previous findings of a mosaic of subregions. The single map also provides a possible organizing principle. The subregions may differ because they emphasize the types of actions that monkeys tend to make in different regions of space.

## Multimodal neurons and the coding of a margin of safety

In addition to its motor output, the precentral gyrus also receives sensory input presumably for the guidance of movement. One class of precentral neuron has a distinctive type of response to tactile and visual stimuli. These bimodal neurons typically have a tactile receptive field on the face, arm or torso and a visual receptive field adjacent to the tactile receptive field, extending 5–30 cm into the space surrounding the body (Fogassi et al., 1996;

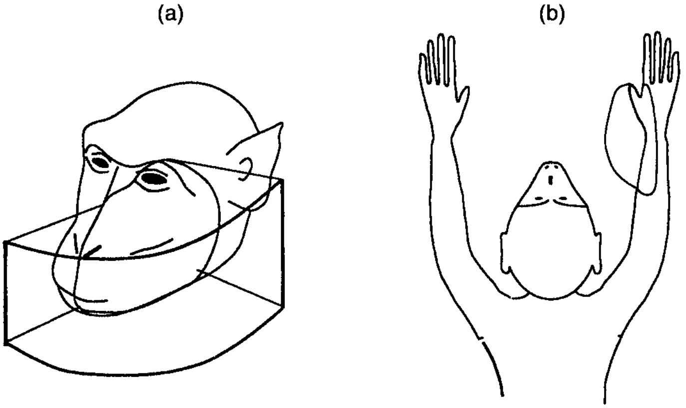

*Figure 9.4* Receptive fields of two bimodal, visual–tactile cells in the polysensory zone. (a) The tactile receptive field (shaded) is on the snout and the visual receptive field (boxed) is confined to a region of space within about 10 cm of the tactile receptive field. Both receptive fields are mainly on the side of the face contralateral to the recording electrode. (b) The tactile receptive field for this neuron is on the contralateral hand and forearm and the visual receptive field surrounds the tactile receptive field.

Graziano et al, 1997; Rizzolatti et al., 1981) (see Figure 9.4). Recently, we found that a subset of these multimodal neurons are trimodal; they have spatially corresponding tactile, visual and auditory receptive fields (Graziano et al, 1999). We found that the multimodal neurons are clustered just posterior to the bend in the arcuate sulcus (Graziano & Gandhi, 2000; see also squares in Figure 9.3). They are concentrated in the dorsal part of F4, within ventral premotor cortex (PMv). Recently we termed this cluster of polysensory neurons the "polysensory zone" (PZ) (Graziano & Gandhi, 2000).

We found that for most of the multisensory neurons, the visual receptive field is anchored to the site of the tactile receptive field. For a cell with a tactile receptive field on the arm, when the arm is moved, the adjacent visual receptive field moves in tandem with the arm; when the eyes or the head move and the arm is stationary, the visual receptive field does not move and remains anchored to the arm (Graziano et al., 1997). For a cell with a tactile receptive field on the face, when the head is rotated, the visual receptive field moves in tandem with the head; when the eyes or the arm move and the head is stationary, the visual receptive field does not move and remains anchored to the head (Fogassi et al., 1996; Graziano et al, 1997). These cells therefore appear to encode the locations of nearby visual stimuli with respect to the body surface, in "body-part-centred" coordinates.

The visual and tactile modalities of these neurons match not only in spatial location but also in directional preference (Graziano et al., 1997;

Rizzolatti et al., 1981). For example, a cell that prefers a rightward moving stimulus in the tactile modality will also prefer a rightward moving stimulus in the visual modality. At least some cells respond preferentially to visual stimuli moving towards the animal on a collision course with the tactile receptive field.

Although the sensory properties of the multimodal neurons have been extensively characterized, their function was unknown. We speculated that they may play a general role in the sensory guidance of movement, contributing to reaching towards, pulling away from, nudging, reaching around and other movements in relation to nearby objects (Graziano et al., 1997; Graziano & Gross, 1998). However, we had no direct evidence for the motor functions of these neurons.

To address the question of function, we electrically stimulated sites within PZ (Graziano et al., 2002). Stimulation elicited movements that were consistent with defending the body against threatening objects. Different movements were evoked depending on the location of the sensory receptive fields. For example, at some sites the neurons had a tactile receptive field on the side of the head and a visual receptive field near the tactile receptive field. Stimulation of this type of site evoked movements consistent with defending the side of the head from an impending threat. These movements included a closure of the eye and facial grimace that was more pronounced on the side of the sensory receptive field; a turning of the head away from the side of the sensory receptive field; a rapid movement of the hand to an upper lateral location as if blocking an object in the sensory receptive field; and a turning outward of the palm (Figure 9.5A). At other sites, the neurons had a tactile receptive field on the arm and a visual receptive field near the arm. Stimulation of this type of site evoked a fast withdrawal of the arm behind the back. These movements resulted in the hand reaching a final position in lower space, generally beside the thigh or hip (Figure 9.5B). Defensive-like movements were obtained even when the monkey was anaesthetized, and thus appeared to be unrelated to the monkey's behavioural context. On the basis of these results, we now suggest that the multisensory neurons within PZ do not serve a general function in the sensory guidance of movement, but instead serve a highly specific function, locating nearby threatening stimuli and organizing the appropriate defensive movements.

Similar neuronal responses to tactile and visual stimuli have been described in area VIP in the parietal lobe. VIP neurons typically have a tactile receptive field on the contralateral side of the face and a visual receptive field that corresponds spatially. (Colby, Duhamel, & Goldberg, 1993; Duhamel, Bremmer, BenHamed, & Gref, 1997; Duhamel, Colby, & Goldberg, 1998; Schaafsma & Duysens, 1996). About half of the neurons respond best to nearby visual stimuli, within 30 cm of the tactile receptive field (Colby et al., 1993). The tactile and visual modalities generally share the same directional preference (Colby et al., 1993). For about half the neurons, the visual receptive field remains stationary in space when the eyes move, and is presumed to

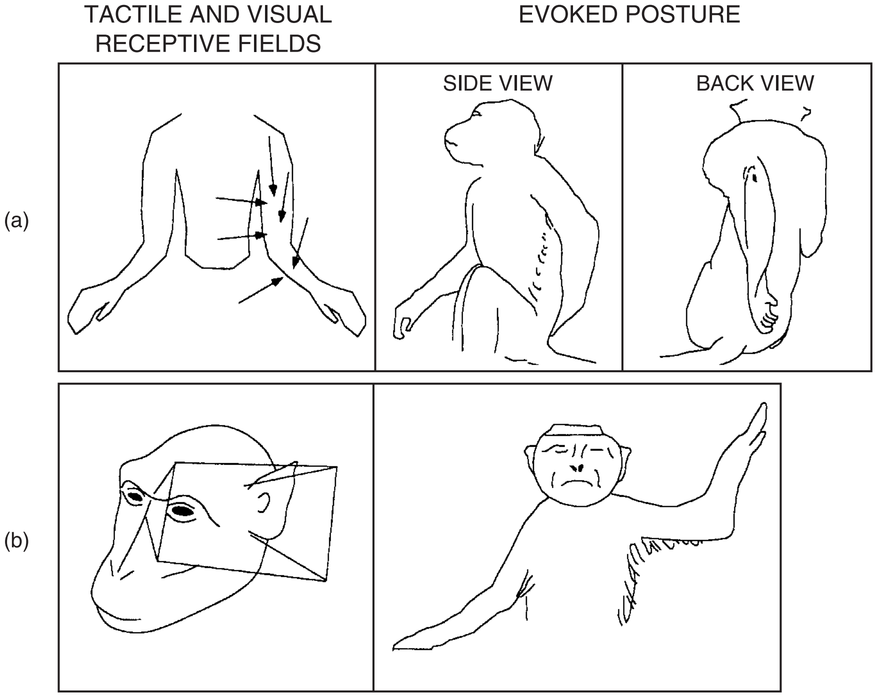

*Figure 9.5* Defensive movements evoked from sites in area PZ. (a) Neurons at this site responded to a touch on the arm (within the shaded area) and to nearby visual stimuli moving towards the arm (indicated by arrows). Microstimulation caused the arm to move to a posture behind the back. (b) Multineuron activity at this site responded to a touch on the contralateral upper part of the face and to visual stimuli in the space near this tactile receptive field. Microstimulation evoked a complex defensive posture involving a facial squint, a head turn, and the arm and hand moving to a guarding position. Adapted from Graziano et al. (2002).

be anchored to the head (Duhamel et al., 1997, 1998). Thus almost identical response properties have been found in VIP and PZ, although the proportions of cell types are somewhat different. This similarity is especially interesting because VIP projects to the premotor cortex, and its main area of projection appears to be PZ (Lewis & Van Essen, 2000; Luppino, Murata, Govoni, & Matelli, 1999).

We recently found that stimulation of area VIP evoked defensive movements similar to those evoked by stimulation of area PZ (Cooke, Taylor, Moore, & Graziano, 2002). Stimulation of cortex surrounding area VIP did not evoke the same movements. Figure 9.6A shows video frames of a defensive movement evoked by electrical stimulation of a site in area VIP. The figure shows a short latency closure of the eye and lifting of the upper lip on the side of the face contralateral to the recording electrode. Figure 9.6B

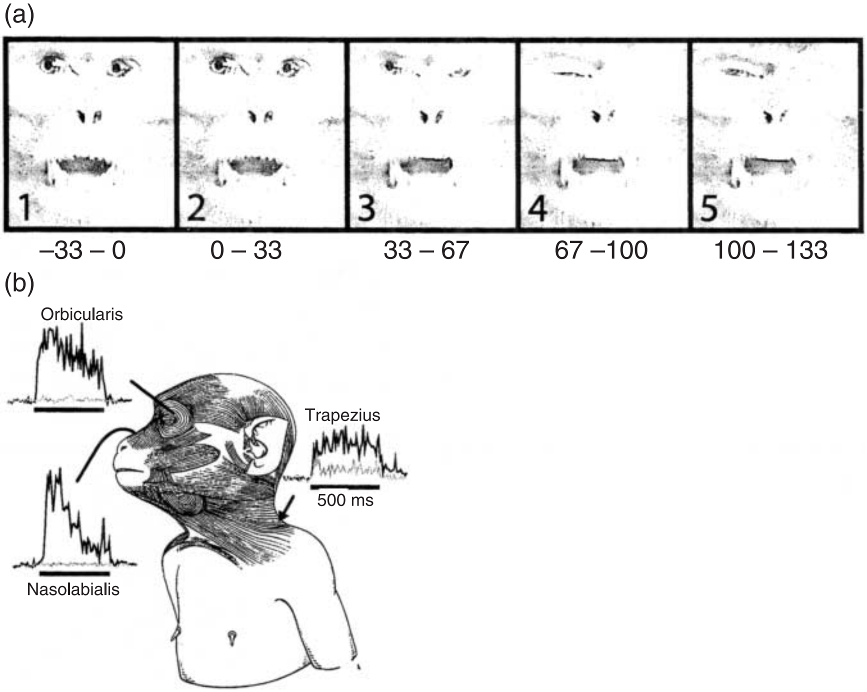

*Figure 9.6* Defensive movements evoked by stimulation of parietal area VIP. (a) An example of a facial flinch evoked by microstimulation of VIP. Images captured from video at 30 frames per second. Numbers beneath each frame indicate time in milliseconds relative to stimulation onset. By frame 3, the monkey's left eye (contralateral to stimulation) began to close and the left upper lip began to lift exposing the teeth. By frame 4, the lifting of the skin on the left snout was more pronounced, deforming the left nostril. The left eye was closed the right eye was partially closed and the left brow had lowered. Stimulation of this site also caused the ear to pull back and down and the left arm to move to the left. Stimulation at 200 μA for 500 ms. (b) EMG activity evoked by stimulation of an example site in VIP. EMG from orbicularis oculi muscle causing squint; nasolabialis muscle causing lifting of upper lip and facial skin; trapezius muscle causing shoulder shrug. Dark lines = EMG from muscles on the left side of body (contralateral to stimulation); light lines = EMG from muscles on the right side of body. Shoulder shrug was bilateral but stronger on the left side. Each EMG trace is the mean of 15 trials rectified and integrated in 10 ms bins. Horizontal line = stimulation period; y-axis in arbitrary units.

shows the EMG traces from three muscles during a stimulation-evoked flinching movement.

One hypothesis is that areas VIP and PZ form part of a pathway that is specilaized for encoding nearby space and defending the body.

## Postural coding as a general method of movement control

The idea of movement control by means of postural coding is not new. It has been particularly successful in the study of speech and of facial expressions. In speech, each phoneme may be defined by a posture of the vocal tract, including the mouth, tongue and larynx (Fowler, Rubin, Remez, & Turvey, 1980). To produce a phoneme, the speaking apparatus moves towards this final posture. It does not need to achieve the final posture, but only to move towards it. For example, in this view a given vowel "is an equivalence set of gestures that are equivalent because they all aim toward some particular limiting shape and length of the vocal tract" (Fowler et al., 1980). Speech is composed of a sequence of these gestures towards defined postures. Why should speech have evolved in this fashion? One possibility is that the mechanisms for speech were built on a pre-existing mechanism for motor control, one that emphasized the specification of complex, behaviourally useful postures. When we stimulated in the ventral part of the precentral gyrus, in the mouth and face representation, we often caused the lips and tongue to move towards specific postures (Graziano et al., 2002). For example, at one site, stimulation caused the mouth to open about 2 cm and the tongue to move to a particular location in the mouth. Regardless of the starting posture of the tongue or jaw, stimulation evoked a movement towards this final configuration. This type of posture may be useful to a monkey for eating, but could also be an evolutionary precursor to the phoneme.

Facial expressions appear to be controlled in a manner strikingly similar to the phonemes in spoken language. An emotional expression is conveyed by the movement of the facial musculature towards a particular posture (Ekman, 1993). A frown, a smile, an angry expression, a surprised expression, a disgust face, all these can be categorized by their archetypal final postures. However, even a subtle movement towards this postural endpoint will vividly convey an emotion to the viewer. Thus, again, the system appears to operate by means of a repertoire of complex postures towards which movements are made.

Could limb movements also be controlled at some level by means of a stored set of postures? Rosenbaum, Loukopoulos, Meulenbroek, Vaughan, and Engelbrecht (1995) proposed a model for limb control that uses linear combinations taken from a basis set of stored postures. The map of postures that we evoked by electrical stimulation in motor cortex could provide a basis for this method of limb control. The map in motor cortex is similar to a map of leg postures evoked by electrical stimulation of the spinal cord in frogs and rats (Giszter, Mussa-Ivaldi, & Bizzi, 1993; Tresch & Bizzi, 1999); thus the spinal cord might also control movement partly at the level of posture.

In motor control, there is a subtle but important distinction between specifying a final posture and specifying a trajectory that is aimed towards a final posture. An example of a control algorithm that specifies only the final posture is the equilibrium position hypothesis. According to this hypothesis, limb movement is controlled by specifying only a final set of muscle tensions (Bizzi, Accornero, Chapple, & Hogan 1984). If the muscles acquire that set of tensions and maintain them in a steady state, the limb will move to the desired final posture and remain there. The equilibrium position hypothesis is now known to be incorrect. During a limb movement to a specified posture, the muscles do not acquire a fixed set of tensions, but rather perform a complex dance of activity, resulting in a smooth path (Bizzi et al., 1984; Brown & Cooke, 1990; Hallett, Shahani, & Young, 1975; Morasso, 1981). This complex pattern of muscle activity depends on both the initial and final position of the arm. Thus the entire trajectory of the arm is specified, not only the desired final configuration.

The stimulation-evoked postures that we found in motor cortex follow the pattern of muscle activation observed during normal movement, rather than the pattern predicted by the equilibrium position hypothesis. Stimulation evokes a complex pattern of muscle activity in the upper arm that resembles the interplay between agonist and antagonist muscles observed during natural movement. This pattern of muscle activity depends on the starting position of the arm. Thus stimulation specifies more than just a final posture; it specifies the entire, coordinated trajectory that is aimed towards the final posture.

## A final caveat

A final caveat is in order. Motor cortex is obviously highly complex, and may control movement by means of many overlapping strategies. This complexity is reflected in the diverse effects of stimulation, including movement of the hand to a location in space, movement of joints towards a final posture, movement at different speeds, and an emphasis on controlling the hand and fingers in certain regions of cortex. At the single neuron level, even more diversity has been found in coding schemes for movement. The coding scheme may even vary depending on the type of movement or the part of the map studied. For example, the manipulation of objects may employ a specialized anatomical and physiological machinery in which the cortex exerts an especially direct control over spinal motor neurons. It is probably incorrect to assign a single motor-control algorithm to motor cortex. Here we suggest that one of possibly many strategies used by motor cortex involves a topographic map of postures that are of behavioural relevance to the animal.

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