CHAPTER 3

A SYSTEM OF MULTIMODAL AREAS IN THE PRIMATE BRAIN

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Introduction

In this chapter we suggest that a set of interconnected areas in the primate brain monitors the location and movement of objects near the body and controls flinch and other defensive responses. This hypothesized 'defensive' system, shown in Fig. 3.1 in a side view of the monkey brain, includes the ventral intraparietal area (VIP), parietal area 7b, the polysensory zone (PZ) in the precentral gyrus, and the putamen. These brain areas are monosynaptically interconnected (Mesulam *et al.* 1977; Weber and Yin 1984; Matelli *et al.* 1986; Cavada and Goldman-Rakic 1989*a*,*b*, 1991; Parthasarathy *et al.* 1992). Of the four areas, PZ is closest to the motor output, sending direct projections to the spinal cord (Dum and Strick 1991).

In the following sections we review experimental results on this system of areas and discuss the evidence that they are involved in representing the visual, tactile, and auditory space near the body and in controlling defensive movements. We concentrate mainly on areas VIP and PZ in the monkey brain, which are the most thoroughly studied of the multimodal areas. We then discuss the evidence that the human brain contains a similar set of multimodal areas processing the space near the body (see also Chapters 4 and 10, this volume).

The polysensory zone (PZ)

The precentral gyrus of monkeys contains a restricted zone in which the neurons respond with short latency to tactile, visual, and sometimes auditory stimuli. Here we refer to this functionally distinct region as PZ (the polysensory zone). Its location is shown in Fig. 3.1.

Most neurons in PZ respond to tactile and visual stimuli (Rizzolatti *et al.* 1981; Graziano *et al.* 1994, 1997*a*; Fogassi *et al.* 1996). For these bimodal cells, the tactile receptive field is located on the face, shoulder, arm, or upper torso. For about 95% of the cells, the tactile receptive field is predominantly or only on the side of the body contralateral to the brain hemisphere studied. The visual receptive field for the bimodal cells extends from the approximate region of the tactile receptive field into the

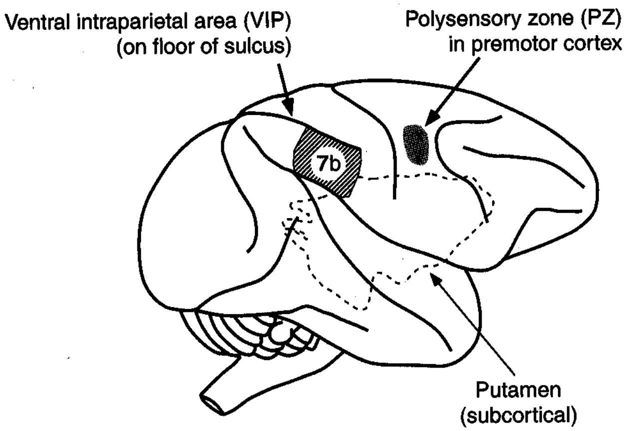

Fig. 3.1 Side view of a macaque monkey brain showing the location of four interconnected multimodal areas.

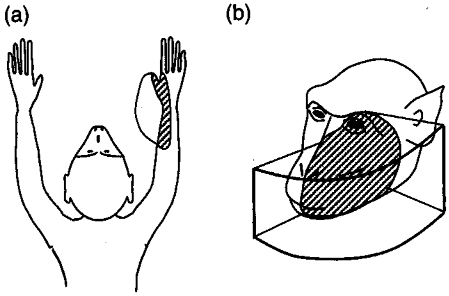

Fig. 3.2 Two examples of bimodal, visual–tactile neurons from premotor cortex. In both cases the tactile receptive field (shaded) matched the location of the visual receptive field (outlined).

immediately adjacent space. For almost all cells (93%), the visual receptive field is confined in depth (Graziano *et al.* 1997*a*). The outer distance of the visual receptive field is usually less than 20 cm. Most of the bimodal cells are directionally selective (Graziano *et al.* 1997*a*). All directions of motion are represented; different cells prefer movement to the left, right, up, down, and even movement of objects toward or away from the monkey. The directional preference is the same for both the tactile and the visual modality for about 80% of the neurons. For example, a cell that prefers the sight of a nearby object moving to the right may also prefer the felt movement of an object, in the same direction, across the tactile receptive field. Thus these neurons do not merely signal a visual stimulus approaching the tactile receptive field; instead the neurons appear to encode specific details about stimulus movement in a variety of directions. Figure 3.2 shows the tactile receptive fields (stippled) and the associated visual receptive fields for two typical bimodal neurons related to the arm (Fig. 3.2(a)) and face (Fig. 3.2(b)).

For almost all bimodal cells with a tactile receptive field on the arm, when the arm is placed in different positions the visual receptive field moves with the arm (Graziano *et al.* 1994, 1997*a*; Graziano 1999). In contrast, when the eyes move, the visual receptive field does not move, but remains anchored to the arm (Gentilucci *et al.* 1983; Fogassi *et al.* 1992, 1996; Graziano *et al.* 1994, 1997*a*; Graziano and Gross 1998). These cells therefore encode the locations of nearby visual stimuli with respect to the arm. Such information could be used to guide the arm away from nearby objects. Figure 3.3 shows an example of data collected from one neuron with a tactile receptive field on the hand and forearm and a visual receptive field that surrounded the tactile receptive field. A ping-pong ball mounted on the end of a robot arm was moved toward the monkey on four different trajectories while the response of the neuron to this visual stimulus was recorded. The neuron responded best to visual stimuli near the arm. When the arm moved, the preferred location for the visual stimulus also moved. Note that when the hand was placed across the midline, the region of best visual response was actually dragged across the midline in correspondence with the hand.

Similarly, for most bimodal cells with a tactile receptive field on the face, when the head is rotated, the visual receptive field moves with the head (Graziano *et al.* 1997*a*, *b*). When the eyes move, the visual receptive field does not move, but remains anchored to the head (Gentilucci *et al.* 1983; Fogassi *et al.* 1992, 1996; Graziano *et al.* 1994, 1997*a*; Graziano and Gross 1998). Such visual receptive fields encode the locations of nearby stimuli relative to the head, and would be useful for guiding the head away from an impending threat. Figure 3.4 shows an example of a neuron with a tactile receptive field on the face and a visual receptive field confined to the space near the tactile receptive field. As shown in this figure, the visual receptive field remains anchored to the face and does not move when the eyes or the arm are moved. When the head is moved, the visual receptive field moves with it.

Neurons in PZ with a tactile receptive field on the side and back of the head often respond to auditory stimuli near the head, within about 30 cm (Graziano *et al.* 1999). Regardless of the intensity of the sound, if the source is more than about 30 cm from the head these neurons respond weakly or do not respond at all. Auditory responses were never found in association with tactile responses on the arm though the reason for this is not clear.

About 20% of the multimodal neurons in PZ continue to respond to objects that were presented in the visual receptive field even after the lights are turned out and the object is no longer visible (Graziano *et al.* 1997*b*). Such neurons apparently 'remember' the locations of nearby objects. When the lights turn on, revealing the presence of an object in the visual receptive field, the neuron will begin to respond. When the lights turn off, the neuron will continue to respond for at least 5 seconds and possibly longer. When the lights turn on again, revealing the absence of the object in the receptive field, the response stops. The firing of these neurons therefore reflects the most recent visual information about the presence or absence of the object near the face.

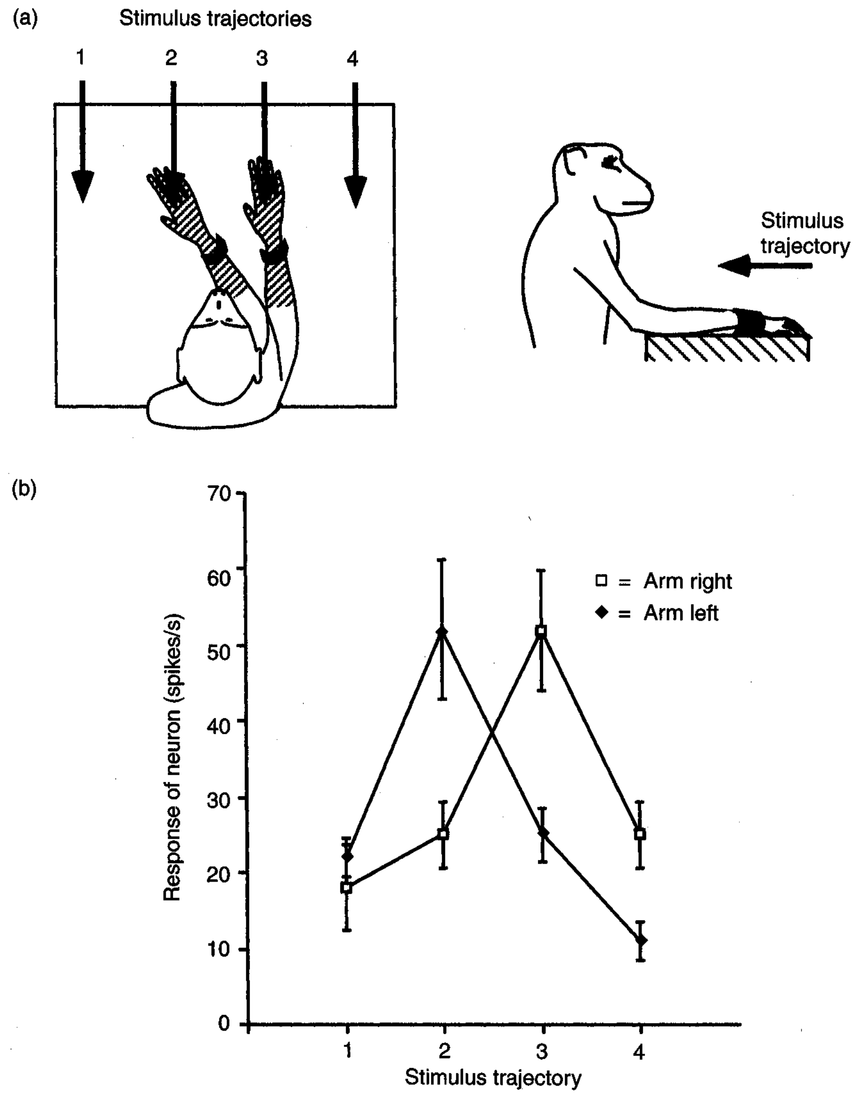

Fig. 3.3 Visual responses of a typical neuron from the premotor polysensory zone (PZ). This neuron had a tactile receptive field (stippled) on the forearm and hand and a visual receptive field within 10 cm of the tactile receptive field. (a) On each trial, the arm contralateral to the neuron was fixed in one of two positions and the visual stimulus (a ping-pong ball mounted on the end of a robot arm) was advanced along one of four trajectories. (b) Responses of the neuron to the four stimulus trajectories. When the arm was fixed on the right, the response was maximum at trajectory 3. When the arm was fixed on the left, the maximum response moved to the left, to trajectory 2.

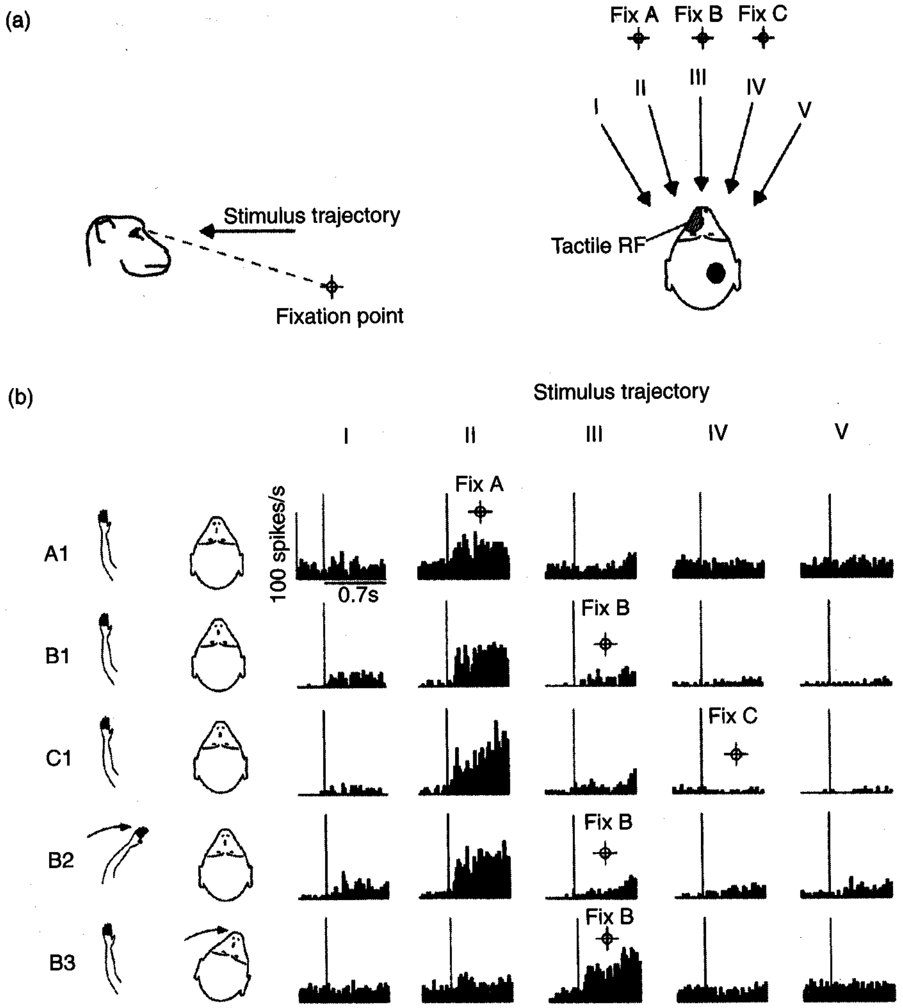

Fig. 3.4 Visual responses of a typical neuron from the premotor polysensory zone (PZ). This neuron had a tactile receptive field (RF) on the cheek and a visual receptive field within about 10 cm of the cheek. (a) Experimental paradigm for testing the effect of head, arm, and eye position. The monkey fixated one of three lights (Fix A, Fix B, or Fix C) spaced 15° apart. The visual stimulus was presented along one of five trajectories (I–V). The monkey's head was held straight (shown), or rotated 15° to the right or the left. The arm was strapped to a movable holder and held straight ahead or bent rightward across the chest. The black dot in the right diagram indicates the hemisphere recorded from. The stippling indicates the tactile receptive field of the cell whose responses are illustrated in (b).
(b) Histograms of neuronal activity, summed over 10 trials, as a function of eye position (Fix A, Fix B, Fix C), stimulus trajectory (I–V), arm position (to the right in B2, to the left in all other conditions), and head position (to the right in B3, straight in all other conditions). The vertical lines indicate stimulus onset. When the head was straight (A1, B1, C1, B2), the neuron responded best to stimulus trajectory II, regardless of eye or arm position. When the head was rotated 15° to the right (B3), the neuron responded best to trajectory III. Thus, the visual receptive field moved toward the right with the head. The spontaneous activity was greatest when the eyes were angled 15° to the left of the head (A1 and B3).

In summary, the multimodal neurons in PZ represent the space immediately surrounding the body through touch, audition, vision, and even memory. These neurons monitor the location and movement of nearby objects.

Electrical stimulation of the polysensory zone

The function of the polysensory neurons in PZ has been the subject of speculation for 2 decades. Rizzolatti and colleagues (1981) first suggested that the multimodal neurons help to guide movement on the basis of sensory input. We expanded Rizzolatti *et al.*'s suggestion, hypothesizing that the neurons guide individual body parts toward or away from nearby objects, such as for flinching, kissing, reaching, or ducking (Graziano *et al.* 1997*a*). Recent results from mapping the precentral gyrus, however, suggest that the multimodal neurons are unlikely to have such a general role in the control of movement (Graziano and Gandhi 2000). As shown in Fig. 3.1, the multimodal cells are clustered in a small zone in the center of the precentral gyrus, whereas limb and body movement is represented by the entire precentral gyrus. We set out to test the motor output of this restricted polysensory zone by electrically stimulating sites within it (Graziano *et al.* 2002). For each cortical site tested, we advanced a microelectrode into the cortex and first studied single-neuron and multineuron activity. We then passed current through the same electrode. We used a train of biphasic pulses, typically at 200 Hz, 25–150 μA, and 0.5 s train duration. Such electrical stimulation directly activates a cluster of neurons around the tip of the electrode. The neuronal activity then spreads to other neurons through transsynaptic signals. Thus, the effect of electrical stimulation is thought to depend on the recruitment of physiologically relevant brain circuits.

Before electrical stimulation, we studied single-neuron and multineuron activity at each site. The results from one sample site are shown in Fig. 3.5(a). When the eyes were covered, the neurons responded to touching the left arm. When the eyes were uncovered, the neurons also responded to the sight of objects near and approaching that arm. We then electrically stimulated the neurons at 200 Hz, 100 μA for 0.5 s. During each stimulation train, the arm moved rapidly to a posture behind the monkey's back. This linking of a response to nearby objects approaching the arm with a motor output that withdraws the arm suggests that these neurons help to guard the arm from an impending threat. Regardless of the initial position of the arm, stimulation always evoked this final 'guarding' posture. The electrically induced movement was indistinguishable from the monkey's own spontaneous withdrawl of the arm from an impending threat, such as when the experimenter lunged rapidly toward the arm as if to grab it.

Another example is shown in Fig. 3.5(b). When the eyes were covered, the neurons at this site responded to touching of the left temple. When the eyes were open, the neurons responded to the sight of objects in the space near that temple. Electrical stimulation of this site caused the left eye to close entirely, the right eye to close partially, the face to contract into a grimace, the head to turn toward the right, the left arm to extend

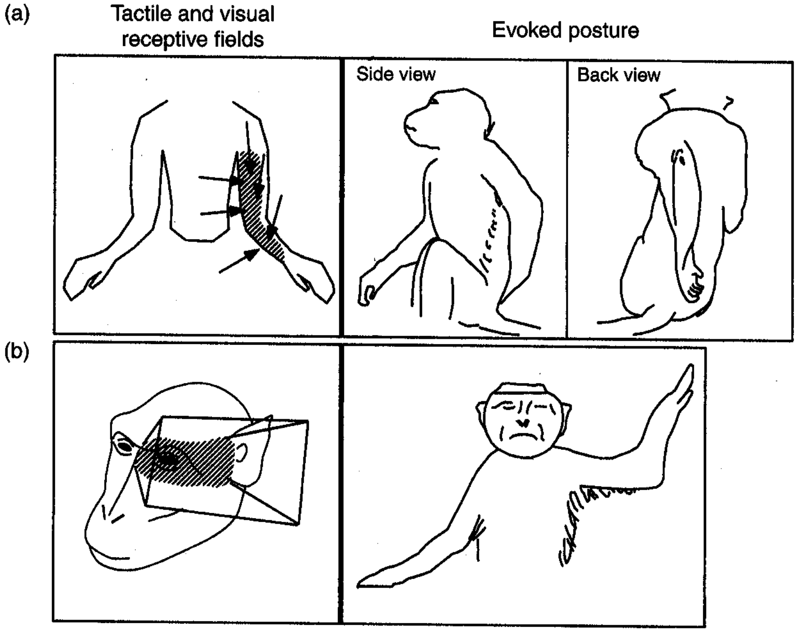

Figure 3.5 Electrical stimulation of PZ evokes defensive movements. (a) Neurons at this site responded to a touch on the arm (within the shaded area) and to nearby visual stimuli moving toward the arm (indicated by arrows). Microstimulation caused the arm to move to a posture behind the back. (b) Multineuron 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.

rapidly into the upper left space, and the left hand to turn such that the palm faced outward. That is, stimulation caused the monkey to mimic the actions of flinching from an object near the side of the head and thrusting out a hand to fend off the object. Stimulation using lower currents evoked a weaker defensive reaction. At the lowest current that was above threshold, only a closure of the eye occurred. This finding suggests that the strength of the flinch response is determined by the amount of neuronal activation in PZ. One possibility is that the salience of a nearby sensory stimulus will determine the magnitude of the neuronal response, which in turn will determine the strength of the flinching movement.

At another site, the neurons responded to a touch on the forehead and to the sight of objects approaching the forehead. Stimulation of that site caused the eyes to close and the head to pull downward. At yet another site, the neurons responded to touching the back of the arm near the elbow and to the sight of objects moving in the periphery. Stimulation caused the elbow to pull rapidly forward and inward toward the midline.

For all 50 sites that we tested within the multimodal zone, in two monkeys, the evoked postures were consistent with flinching, avoiding, or defending against an object located in the multimodal receptive field. Stimulation of sites in the precentral gyrus outside the multimodal zone did not evoke defensive postures, but instead evoked a different class of movements, such as reaching movements, shaping of the hand into grip postures, or movements of the tongue and jaw.

Does the electrical stimulation induce a sensation, such as pain on a part of the body, thereby causing the monkey to flinch in reaction to that sensation? We believe that this is not the case. Instead, the stimulation appears to evoke a specific motor plan devoid of any sensory component or emotional valence. Three observations may support this view. First, the evoked movements generally had latency of less than 33 ms, probably too short a time for the monkey to react intentionally to an electrically induced sensation. Second, after each stimulation, as soon as the stimulation train ended, the monkey returned to a normal resting posture or to feeding itself pieces of fruit. No lingering distress was evident. Third, we found that the same defensive movements could be elicited from an anesthetized monkey. For several stimulation sites, we tested the effect of stimulation in the awake preparation, then injected the monkey with an anesthetic (nembutal and/or ketamine) and waited until the animal was unresponsive. To ensure that the monkey could not flinch from externally applied stimuli, we touched the monkey, manipulated the limbs, blew on the face, and finally pricked the eyelid. None of these stimuli elicited a response from the anesthetized monkey, suggesting that the monkey was not reacting to normally startling or painful stimuli. Electrical stimulation of the bimodal site, however, elicited a flinching movement including a facial grimace and clenching shut of the eyelids. This finding suggests that the stimulation does not operate indirectly by way of a sensory percept, but instead directly stimulates a motor output.

Area PZ projects directly to the spinal cord and to primary motor cortex (Dum and Strick 1991). We suggest that PZ lies near the end of a specialized, sensorimotor pathway that detects and locates threatening objects near the body and specifies the appropriate postures to defend the body. In the next section we describe area VIP, a multimodal area in the parietal lobe that may be a major source of input to PZ.

The ventral intraparietal area (VIP)

Most neurons in area VIP (see Fig. 3.1 for location) are bimodal, responding to tactile stimuli on the face and to visual stimuli near the face (Colby *et al.* 1993; Duhamel *et al.* 1998). Some cells respond to visual stimuli only within a few centimeters of the tactile receptive field, while others respond to more distant stimuli. Most cells are directionally selective in both modalities, and the preferred direction in the tactile modality almost always matches the preferred direction in the visual modality. Some neurons in VIP are even tuned to motion toward the animal, that is, to an expanding visual stimulus; other neurons prefer a contracting visual stimulus (Schaafsma and Duysens 1996). This directional selectivity of neurons in VIP may be related to the strong input to VIP from the middle temporal visual area MT (Maunsell and Van Essen 1983*a*). Area MT is thought to be specialized for the processing of visual motion; most of its neurons respond to moving visual stimuli and are tuned to the direction of movement (e.g. Allman and Kass 1971; Dubner and Zeki 1971; Maunsell and Van Essen 1983*b;* Albright 1984).

At least some VIP neurons are trimodal, responding to visual, tactile, and auditory stimuli. For these neurons, the three receptive fields are typically spatially aligned (Schlack *et al.* 2000).

Thus far, the properties of neurons in area VIP are identical to those in PZ. However, in one major respect the two areas differ. In PZ, the visual receptive fields of almost all neurons are anchored to the body surface. Some visual receptive fields are anchored to the arm, moving as the arm moves; others are anchored to the head, moving as the head moves. When the eyes move, the visual receptive fields do not move. In VIP, however, most visual receptive fields are anchored to the retina and move with the eyes; only a minority are stable in space when the eyes move (Duhamel *et al.* 1997). Some visual receptive fields in VIP appear to be intermediate in nature, moving in the same direction as that in which the eyes move but not to the same extent. This mixture of properties suggests that VIP is an intermediate step in the transformation from retinocentric visual receptive fields to the body-part-centered receptive fields found in PZ.

Several groups have created neural network models that transform retinal receptive fields into head- or arm-centered receptive fields (Zipser and Andersen 1988; Pouget *et al.* 1993; Salinas and Abbott 1995; see Chapter 6, this volume for a different approach). These neural network models have somewhat different properties, but they all demonstrate certain underlying constraints.

1. In order to construct a head-centered visual receptive field, it is necessary to combine visual information with information (e.g. motor feedback) about eye position. In order to construct a limb-centered visual receptive field, it is necessary to use additional information (e.g. proprioceptive) about the position of the head on the trunk and the limb with respect to the trunk. These visual and proprioceptive signals are known to converge on areas in the parietal lobe, including area VIP.
2. When visual information and proprioceptive information converge on a single simulated neuron, the neuron often has complex and intermediate response properties such as a visual receptive field that is modulated by eye position, or that shifts partially with the eye, similar to the properties actually found in area VIP.

We suggest that the system of bimodal areas is organized in a hierarchy. According to this suggestion, visual, tactile, and auditory information first converge in VIP. This multimodal information is further processed in PZ, where the neurons respond on the basis of the proximity of objects to specific body parts. If the stimulus is sufficiently salient, that is, if the neurons are sufficiently activated, the circuit will trigger the appropriate defensive movement by means of the projections from PZ to the spinal cord (Dum and Strick 1991) and other motor structures.

We have now electrically stimulated sites within area VIP and evoked defensive movements similar to those evoked by stimulation in PZ. These evoked movements resemble the natural movements made by the monkey when defending itself against a nearby object in the location of the multimodal receptive fields found at the stimulated site. In contrast, stimulation of cortex immediately surrounding VIP did not evoke defensive movement (Cooke *et al.* 2003).

Area 7b

Multimodal responses similar to those found in PZ and VIP have been reported in other brain areas including parietal area 7b (Hyvarinen and Poranen 1974; Leinonen and Nyman 1979; Leinonen *et al.* 1979; Robinson and Burton 1980*a*, *b;* Hyvarinen 1981; Graziano and Gross 1995). This area, shown in Fig. 3.1, is monosynaptically connected to VIP and PZ and may be part of the same brain system, though it has not been as intensively studied.

In area 7b, neurons typically have a tactile receptive field on the arms, face, or torso. Almost all of these neurons have large receptive fields covering more than one body part. In some cases, the receptive fields cover the entire body. About 35% of the neurons are also visual. These visual receptive fields roughly match the location of the tactile receptive field. The visual responses are strongest in the space near the body (within about 50 cm). Trimodal neurons, responding to visual, tactile, and auditory stimuli, have been found in at least one part of 7b, in the upper bank of the lateral sulcus (Graziano, unpublished observations). These trimodal cells generally have a large tactile receptive field covering half or all of the body, a large visual receptive field including the entire field of view, and a response to sounds generated near the head, within about 50 cm. These response properties are similar to the responses found in VIP and PZ, except that the receptive field size is generally larger in 7b.

We tested whether the visual receptive fields in 7b were anchored to the retina or to the body surface. We plotted visual receptive fields while the monkey fixated different locations and found that, for most cells, the visual receptive field moved with the eye (Hu *et al.* 1998). For some cells, this movement was partial—the receptive field did not move to the same extent that the eye moved. For a minority of cells, the visual receptive fields did not move, but instead remained stationary when the eyes moved. For bimodal neurons with a tactile receptive field on the arm, when the arm was moved to different locations, the visual receptive field did not move with the arm (Graziano and Gross 1995; Graziano *et al.* 1996). These results suggest that the visual receptive fields in 7b, like those in VIP, are intermediate in nature between a retinal coordinate system and a coordinate system fixed to the body surface.

The putamen

The putamen is a large subcortical structure that forms the lateral part of the basal ganglia (see Fig. 3.1). Neurons in the putamen respond to tactile stimuli and also during voluntary movements. These tactile and motor fields are arranged to form a map of the body, with the legs represented at the top of the putamen and the inside of the mouth represented at the bottom (Crutcher and DeLong 1984*a*, *b*; Liles 1985; Alexander 1987; Schultz and Romo 1988; Kimura *et al.* 1992). In the arm and face part of the map, about 25% of the neurons are also visually responsive (Graziano and Gross 1993). For these bimodal, visual–tactile neurons, the visual receptive field is confined to the space near the body, within about 20 cm, and matches the location of the tactile receptive field on the face or arm. For bimodal cells with a tactile receptive field on the arm, when the arm is moved to different locations, the visual receptive field also moves, remaining in register with the arm. An example is shown in Fig. 3.6. This neuron responded to tactile stimulation on the hand and to the sight of objects in the space near the hand. When the hand was moved to different locations the visual receptive field also moved, thus remaining anchored to the hand. Because these studies of visual responses in the putamen were done in anesthetized monkeys with a fixed eye position, it is not known how eye position affects the visual receptive fields. Auditory responses have not yet been studied in the putamen.

Multimodal areas in the human brain

Recent evidence suggests that the human brain contains a set of multimodal areas much like the ones described above for the monkey brain (see Chapter 10, this volume). In one experiment (Bremmer *et al.* 2001), participants in a magnetic resonance imaging (MRI) scanner were exposed to tactile, visual, and auditory stimuli on separate trials. A small set of cortical areas appeared to be multimodal, that is, they could be activated above baseline by any of the three sensory modalities. One of the multimodal areas was located in the parietal lobe, on the floor of the intraparietal sulcus, closely matching the location

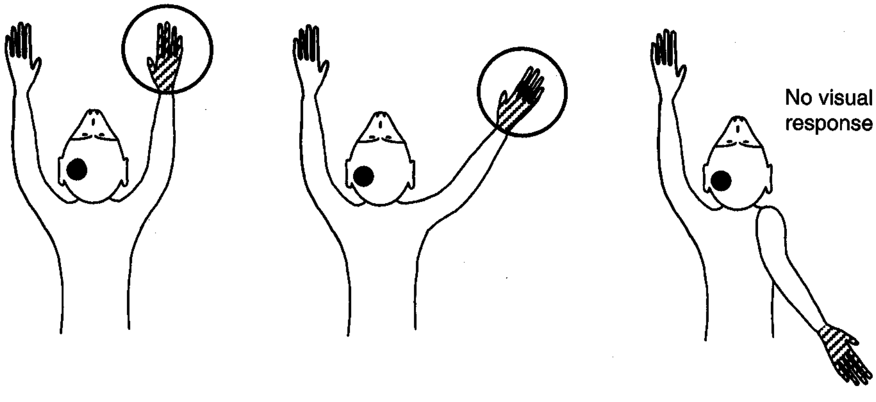

Fig. 3.6 Tactile receptive field (shaded) and visual receptive field (circled) of a neuron from the putamen studied in an anesthetized monkey with eye position fixed. The visual receptive field was anchored to the tactile receptive field, moving as the hand moved. The cell did not respond to visual stimuli when the hand was out of view behind the monkey's back.

of area VIP in the monkey brain. A second multimodal area was located in the frontal lobe, just in front of the central sulcus, closely matching the location of PZ in the monkey brain. A third multimodal area was located in the upper bank of the lateral sulcus. The correspondence to the monkey brain is less clear in this case, but this region of the human brain might correspond to part of area 7b in the monkey brain. Alternatively, it might represent a new multimodal area not yet found in the monkey brain. Deep structures, such as the putamen, were not investigated in this human study.

In another study (Vallar *et al.* 1999), human participants in an MRI scanner made judgements about the location of a visual stimulus with respect to the head or, in control trials, about the movement of the stimulus. The task that required referencing spatial locations to the body activated an area in the frontal lobe closely matching PZ in the monkey brain.

These brain imaging studies suggest that the human brain may contain a set of multimodal cortical areas, many of which match the location of the multimodal areas in the monkey brain. It will be important to test if these areas in the human brain are engaged during tasks that tap into a defensive or flinch mechanism.

Attention to space near the body in humans

In humans, attention to the space near the body may be partly separate from attention to the space far from the body. In studies of humans with unilateral (typically right-hemisphere) lesions of the parietal or frontal cortex, attentional neglect of near space or of far space can be demonstrated separately in different patients (Halligan and Marshall 1991; Cowey *et al.* 1994). Many patients also show sensory extinction specific to the space near the contralesional side of the body, usually the left side after a right-hemisphere lesion (di Pellegrino *et al.* 1997; Ladavas *et al.* 1998, 2001; also see Chapter 4, this volume). In these patients, a tactile stimulus presented to the left side of the body will be neglected in the presence of a simultaneous, competing stimulus presented near the body on the right side. The competing stimulus can be visual or auditory, but must be presented in the space near the body to produce maximum extinction.

Attentional effects in near space can also be demonstrated in healthy human participants. For example, a touch on the hand draws visual attention to the area of space around the hand (Driver and Spence 2000; Pavani *et al.* 2000; Spence *et al.* 2001; Chapter 11, this volume). The enhanced region of visual space is anchored to the hand, shifting in space as the hand is placed in different locations, much like the visual receptive fields found in PZ.

Personal space and margin of safety: some final speculations

One hypothesis is that the multimodal neurons in PZ, VIP, and perhaps other brain areas underlie attention to nearby space. How could the multimodal neurons serve both a general attentional function for nearby space and a limited motor function for defending the body? We speculate that the defense of the body from nearby objects is not a limited function, but rather a pervasive operation that occurs at all times and influences most behaviors as well as the focus of our spatial attention. For example, when walking into a room, we usually avoid hitting our shoulders on the door frame, our eyes on the corners of book shelves, and our shins on chairs. Even while sitting, our movements are strongly biased to avoid hitting arms, elbows, or head on the normal clutter of nearby objects. The sudden appearance of a stimulus near or touching the body, such as an unexpected tap on the shoulder from behind, can elicit a fast defensive reaction and re-orienting of spatial attention.

We speculate that multimodal brain areas such as PZ and VIP may defend the body mainly by monitoring nearby objects and making subtle adjustments to ongoing movements, biasing those movements away from the trajectory of the nearby object. An extreme stimulus, evoking extreme activation in VIP and PZ, might result in an overt flinch. This speculation helps to explain why any stimulus near the body will cause neurons in VIP and PZ to become active to some extent, even if the monkey does not give an overt flinch in reaction to that stimulus. It also helps to explain why low levels of electrical stimulation in PZ do not evoke an overt flinch, slightly higher levels evoke subtle defensive movements, and yet higher levels of stimulation evoke increasingly stronger defensive movements. That is, the production of overt, strong defensive movements may represent only the extreme end of the operating range of area PZ, VIP, and other multimodal areas. We speculate that our attention to objects within personal space, the natural margin of safety around the body, and the control of defensive movements are all facets of the same underlying multimodal brain system.

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