27 Multisensory Neurons for the Control of Defensive Movements

MICHAEL S. A. GRAZIANO, CHARLES G. GROSS, CHARLOTTE S. R. TAYLOR, AND TIRIN MOORE

Introduction

If a hornet flies toward your face, you might duck, squint, and lift your hand to block it. If the insect touches your hand, you might withdraw your hand, even pulling it behind your back. These defensive movements have a reflexive quality. They are fast and can occur without conscious planning or thought. They are similar in all people (Fig. 27.1; Color Plate 6). Although they seem reflexive, however, defensive movements are also highly sophisticated. They can be elicited by touch, sight, or sound. They involve coordination between different body parts, such as the arm and head. They are spatially specific: the body parts that move and the direction of movement are appropriate for the location of the threat. The movements can be stronger or weaker, depending on external context or the internal state of the person. For example, someone whose "nerves are on edge" may give an exaggerated alerting response to an unexpected stimulus.

What sensorimotor pathways in the brain coordinate this rich and complex behavior? We suggest that a special set of interconnected areas in the monkey brain monitors the location and movement of objects near the body and controls flinch and other defensive responses. This hypothesized "defensive" system, shown in Figure 27.2, 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 (Cavada & Goldman-Rakic, 1989a, 1989b, 1991; Kunzle, 1978; Luppino, Murata, Govoni, & Matelli, 1999; Matelli, Camarda, Glickstein, & Rizzolatti, 1986; Mesulam, Van Hoesen, Pandya, & Geschwind, 1977; Parthasarathy, Schall, & Graybiel, 1992; Weber & Yin, 1984). Of the four areas, PZ is closest to the motor output, sending direct projections to the spinal cord (Dum & Strick, 1991). Electrical stimulation of PZ evokes defensive movements, such as withdrawal of the hand, squinting, turning of the head, ducking, or lifting the hand as if to defend the side of the head (Graziano, Taylor, & Moore, 2002).

In the following sections we review experimental results on this system of areas and discuss the evidence that they are involved in representing the space near the body and in controlling defensive movements. We concentrate mainly on areas VIP and PZ in the monkey brain, because they are the most thoroughly studied of these multisensory areas. We then discuss the general question of coordinate transformations from sensory input to motor output. Finally, we discuss the evidence that the human brain contains a similar set of multisensory areas processing the space near the body.

The brain contains many multisensory areas in addition to the set of areas described in this chapter. These other areas are thought to have a variety of specific functions. For example, the superior colliculus contains neurons that respond to tactile, visual, and auditory stimuli. This structure is thought to be involved in orienting of the eyes, ears, or body toward salient stimuli (see Stein, Jiang, & Stanford, Chap. 15, this volume; Meredith, Chap. 21, this volume; Van Opstal & Munoz, Chap. 23, this volume). Regions of the parietal and premotor cortex appear to be involved in the multisensory task of coordinating hand actions for grasping objects (see Fogassi & Gallese, Chap. 26, this volume; Ishibashi, Obayashi, & Iriki, Chap. 28, this volume). Work in human stroke patients and normal human subjects suggests that multisensory processing is crucial for directing spatial attention around the body (see Spence & McDonald, Chap. 1, this volume). A common view a century ago was that the brain contained association areas, regions that served the general purpose of combining the senses. These association areas did not have specific functions; they provided a general understanding of the environment and helped in choosing a path of action. Work over the past 20 years on multisensory integration paints a different picture, one in which the brain contains many distinct multisensory areas, each with its specific set of functions.

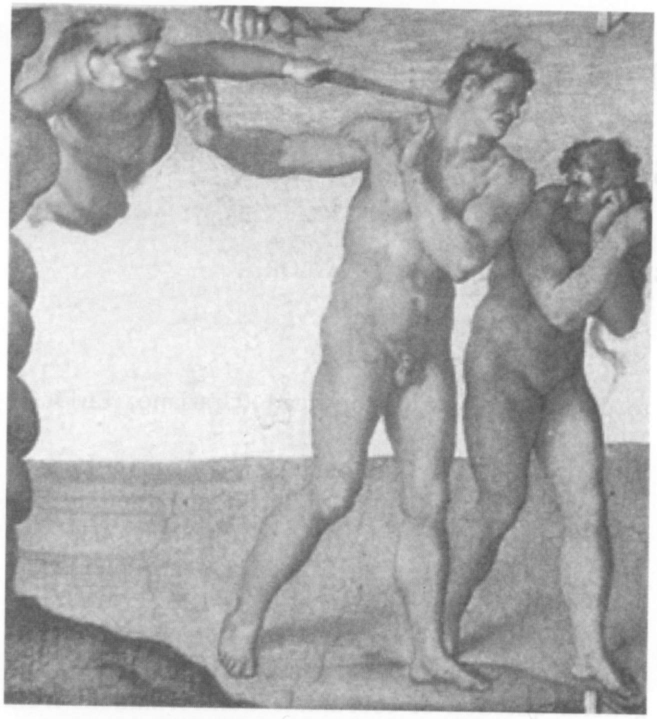

FIGURE 27.1 Detail from Michelangelo's *Fall and Expulsion from Eden.* Both Adam and Eve are in classic defensive poses, with the head turned and the hands raised to defend the face. Compare with Figure 27.5*B*. (See Color Plate 6).

The polysensory zone

The precentral gyrus of monkeys contains a restricted zone in which the neurons respond with short latency to tactile, visual, and sometimes auditory stimuli. This zone is variously termed ventral premotor (PMv) or inferior area 6. Recent mapping experiments (Graziano & Gandhi, 2000) show that the region of multisensory responses does not encompass the entire ventral premotor cortex. Its location varies slightly from monkey to monkey, and whether it lies entirely within premotor cortex is not yet clear. We have therefore adopted a new, more descriptive term, polysensory zone (PZ), to describe this restricted and functionally distinct region (see Fig. 27.2).

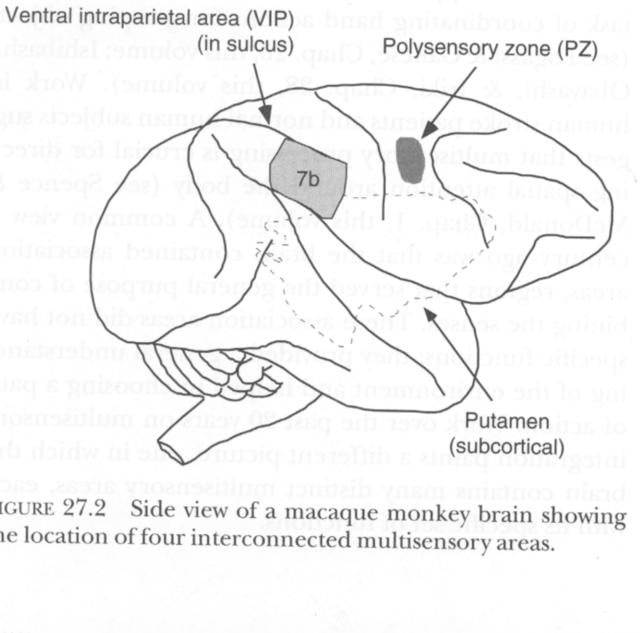

FIGURE 27.2 Side view of a macaque monkey brain showing the location of four interconnected multisensory areas.

Neurons in other parts of motor and premotor cortex also respond to sensory stimuli, especially in animals trained to use those stimuli to perform a task (e.g., Boussaoud, Barth, & Wise, 1993; Kwan, MacKay, Murphy, & Wong, 1985; Mauritz & Wise, 1986). The sensory responses found in PZ, however, do not depend on training the animal. Instead, the neurons respond to passively presented stimuli. The responses can even be found in anesthetized animals (Graziano, Hu, & Gross, 1997a). These sensory responses may derive from the direct projections to PZ from the parietal lobe, especially from areas VIP and 7b (Cavada & Goldman-Rakic, 1989b; Luppino et al., 1999; Matelli et al., 1986). PZ in turn can influence movement through its projections to the rest of the motor cortex and to the spinal cord (Dum & Strick, 1991). PZ therefore is not strictly a sensory or a motor area but, like much of the brain, lies on the pathway from sensory input to motor output.

Most neurons in PZ respond to tactile and visual stimuli (Fogassi et al., 1996; Graziano, Yap, & Gross, 1994; Graziano et al., 1997a; Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981). For these bimodal cells, the tactile receptive field is located on the face, shoulder, arm, or upper torso, and the visual receptive field extends from the approximate region of the tactile receptive field into the immediately adjacent space. For almost all cells (93%), the visual receptive field is confined in depth (Graziano et al., 1997a). The visual receptive fields usually extend out from the body less than 30 cm. Most of the bimodal cells are directionally selective (Graziano et al., 1997a). 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 usually the same for both the tactile and the visual modality. For example, a cell that responds best to the sight of a nearby object moving to the right may also respond best to the felt movement of an object in the same direction, across the tactile receptive field. Figure 27.3 shows the tactile receptive fields and the associated visual receptive fields for two typical bimodal neurons related to the face and arm.

For almost all bimodal cells with a tactile receptive field on the arm, when the arm is placed in different

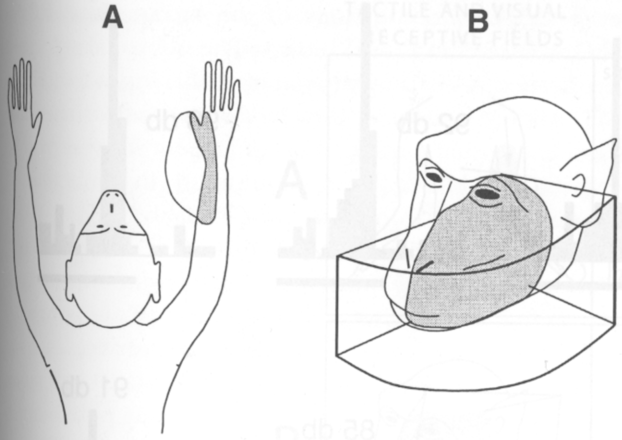

FIGURE 27.3 Two examples of bimodal, visual-tactile neurons from the polysensory zone in the precentral gyrus. In both cases the tactile receptive field (stippled) matched the location of the visual receptive field (outlined). (*A*) Arm; (*B*) face.

positions, the visual receptive field moves with the arm (Graziano, 1999; Graziano, Yap, et al., 1994; Graziano et al., 1997a). In contrast, when the eyes move, the visual receptive field does not move but remains anchored to the arm (Fogassi et al., 1992, 1996; Gentilucci, Scandolara, Pigarev, & Rizzolatti, 1983; Graziano & Gross, 1998; Graziano, Yap, et al., 1994; Graziano et al., 1997a). Thus these cells 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.

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., 1997a, 1997b). When the eyes move the visual receptive field does not move but remains anchored to the head (Fogassi et al., 1992, 1996; Gentilucci et al., 1983; Graziano, Yap, et al., 1994; Graziano & Gross, 1998; Graziano et al., 1997a). 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.

The buzzing of an insect near the ear can sometimes elicit a flinch reaction. Therefore, we might expect neurons in PZ to be responsive to auditory stimuli. Indeed, neurons with a tactile response on the side and back of the head often respond to auditory stimuli near the head, within about 30 cm (Graziano, Reiss, & Gross, 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 not at all. Figure 27.4 shows an example of a cell tested with bursts of white noise presented over a speaker at different distances from the head in the dark. At 10 cm from the head, the white noise evoked a response at all loudness levels. At 25 cm from the head, the sound bursts evoked a smaller response. At 50 cm from the head, the sound bursts evoked little or no response. The auditory parameter that is used by these neurons to encode the distance to the stimulus is not known, but it is thought that primates use the amount of reverberation of sound to estimate the distance to the source (Blauert, 1997). Auditory responses were never found in association with tactile responses on the arm. It may be that auditory localization in nearby space is most precise near the head and is not adequate to determine whether a stimulus is approaching the arm. Thus, a defensive or flinch mechanism might use auditory information mainly to protect the head.

About 20% of the multisensory neurons in PZ continue to respond to objects in the visual receptive field even after the lights are turned out and the object is no longer visible (Graziano et al., 1997b). Such neurons apparently "remember" the locations of nearby objects. When the lights are turned on, revealing the presence of an object in the visual receptive field, the neuron will begin to respond. When the lights are turned off, the neuron will continue to respond. When the lights are turned 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. Such mnemonic information could be useful in maintaining a margin of safety around the body even when the eyes are closed, in the dark, or for objects out of view behind the head. The neuronal signal, essentially "alerting" the motor system to the presence of a stimulus immediately adjacent to the head, could be used for collision avoidance. The effectiveness of this remembered spatial information can be demonstrated by walking toward a wall or other known obstacle in a dark room. One experiences a strong, uneasy compulsion to cringe when the face approaches the remembered location of the object.

In summary, the multisensory neurons in PZ represent the space immediately surrounding the body through touch, audition, vision, and even visual memory. These neurons monitor the location and movement of nearby objects. In the following section we describe the results of electrical stimulation in PZ. These studies suggest that neurons in PZ control a specific type of motor output, namely, movements that protect the body against an impending threat.

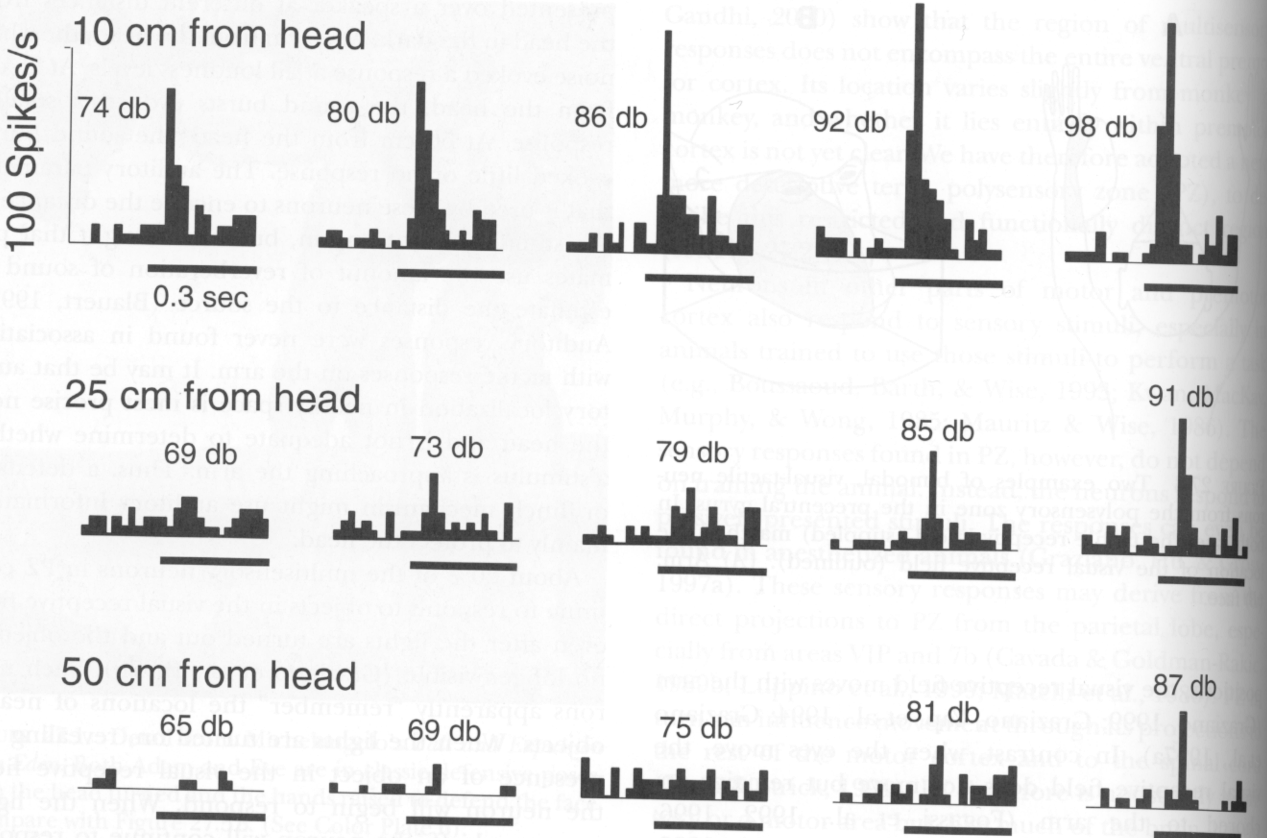

FIGURE 27.4 Auditory responses of a trimodal, visual-tactile-auditory neuron in PZ. This neuron had a tactile receptive field on the right side of the head and a visual receptive field near the right side of the face. It also responded to sounds presented near the right side of the face. Each histogram shows the response of the neuron to white noise presented over a loudspeaker in the dark (average of 10 trials). The intensity of the sound was measured in decibels by a small microphone at the monkey's ear. When the speaker was 10 cm away from the head, the neuron responded to all sound intensities presented. When the speaker was 25 cm from the head, the neuron responded less well. When the speaker was 50 cm from the head, the neuron responded weakly or not at all, regardless of the intensity of the sound.

Electrical stimulation of the polysensory zone

The function of the multisensory neurons in the precentral gyrus has been the subject of speculation for two decades. Rizzolatti and colleagues (1981) first suggested that the multisensory neurons help guide movement on the basis of sensory input. We elaborated on Rizzolatti'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 & Gross, 1995; Graziano et al., 1997a). Recent results from mapping the precentral gyrus, however, suggest that the multisensory neurons are unlikely to have such a general role in the control of movement (Graziano & Gandhi, 2000). The multisensory cells are clustered in a small zone in the center of the precentral gyrus, covering relatively little of the motor representation. What function could be served by this restricted zone? We set out to test the motor output of PZ 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.

The results from one example site are shown in Figure 27.5*A*. Neurons at this site had a tactile receptive field on the left arm and a visual receptive field in space near the left arm. The visual response was strongest to objects approaching the tactile receptive field from any direction, but there was a response to stationary stimuli as well. We electrically stimulated this cortical site at

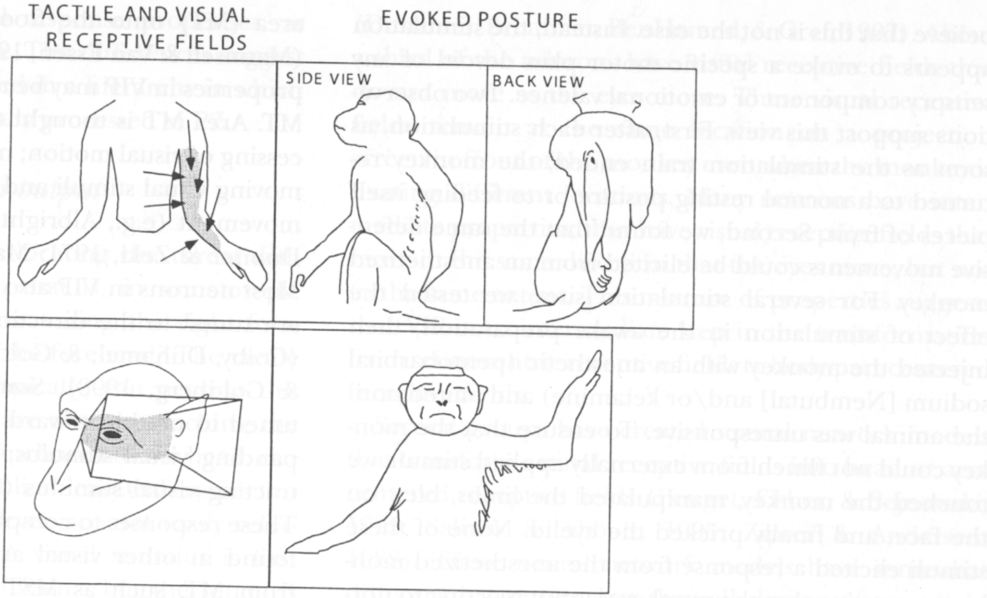

FIGURE 27.5 Electrical stimulation of PZ evokes defensive movements. (*A*) Neurons at this site responded to a touch on the arm (within the shaded area) and to nearby visual stimuli moving toward the arm (indicated by arrows). Microstimulation caused the arm to move to a posture behind the back. (*B*) 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. Compare with Figure 27.1.

200 Hz and 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.

Another example is shown in Figure 27.5*B*. When the eyes were covered, the neurons at this site responded to touching the left temple. When the eyes were open, the neurons responded to the sight of objects in the space near the 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 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 (compare Fig. 27.5*B* with Fig. 27.1.) 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 PZ, in two monkeys, the evoked postures were consistent with flinching, avoiding, or defending against an object located in the multisensory receptive field. These defensive movements usually involved a retraction of body parts from the region of the multisensory receptive field, but in some cases also involved a palm-out thrusting of the hand toward the region of the multisensory receptive field. Thus these evoked movements appeared to include a complex mixture of withdrawal and blocking. Stimulation of sites outside PZ 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 (Graziano et al., 2002).

Does the electrical stimulation cause a sensory percept such as pain on a part of the body, 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. Two observations support this view. First, 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. Second, 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 (pentobarbital sodium [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 that included a facial grimace and a 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.

Is the control of defensive movements the main or only function of area PZ, or does it have other functions, such as the control of reaching and grasping in the space near the body? Thus far, for all multimodal sites that we have tested within PZ, stimulation evoked an apparent defensive movement, not a reach or a grasp. One possibility is that this defensive function is somehow more electrically excitable than other functions, and thus, on stimulation, it dominates. Another possibility is that the defensive function is the main or only function of the brain area. This question remains unanswered, but we hope that studies using reversible deactivation will be able to address the issue in the future. On the basis of the data thus far, we tentatively suggest that PZ is primarily involved in the control of defensive movements.

In the next two sections we discuss areas VIP and 7b in the parietal lobe. Vision, touch, and audition converge in VIP and 7b. These two areas project directly to PZ and may be a source of the multisensory input to PZ. Neurons in VIP and 7b have response properties that are similar to but less complex than the properties in PZ, suggesting that there is a hierarchy of areas that process the space near the body.

The ventral intraparietal area

The ventral intraparietal area (VIP) was first defined as the projection zone of the middle temporal visual area (MT) onto the floor of the intraparietal sulcus (Maunsell & Van Essen, 1983a). The neuronal response properties in VIP may be related to this input from area MT. 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., Albright, 1984; Allman & Kass, 1971; Dubner & Zeki, 1971; Maunsell & Van Essen, 1983b). Most neurons in VIP also respond to visual stimuli and are tuned to the direction of motion of the stimulus (Colby, Duhamel, & Goldberg, 1993; Duhamel, Colby, & Goldberg, 1998). 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 & Duysens, 1996). These responses to complex motion patterns have been found in other visual areas that receive a projection from MT, such as MST and caudal STP (Graziano, Andersen, & Snowden, 1994; Hikosaka, Iwai, Saito, & Tanaka, 1988; Tanaka et al., 1986).

VIP, however, is strikingly different from the other visual motion areas in two respects. First, about half of VIP cells respond best to nearby visual stimuli, usually within 30 cm, sometimes only within a few centimeters (Colby et al., 1993). This preference for nearby stimuli is independent of the size of the stimulus. The depth cues that are used by VIP neurons are not yet known but probably include binocular disparity.

A second property of VIP that sets it apart from other visual motion areas is that almost all of its neurons have a tactile receptive field in addition to a visual receptive field (Duhamel et al., 1998). The tactile receptive field is typically on the face and roughly matches the location of the visual receptive field. Cells with a tactile receptive field on the forehead, for example, tend to have a visual receptive field in upper space, near the forehead. Cells with a tactile receptive field on the chin tend to have a visual receptive field in lower space near the chin. The visual and tactile modalities match not only in location but also in directional preference. For example, cells that prefer a leftward-moving visual stimulus usually also prefer a tactile stimulus that moves leftward across the skin.

At least some VIP neurons are trimodal, responding to visual, tactile, and auditory stimuli; for these neurons, the three receptive fields are spatially aligned (Schlack, Sterbing, Hartung, Hoffmann, & Bremmer, 2000).

In summary, neurons in area VIP receive convergent visual, somesthetic, and auditory input. They encode the location and motion of objects near the body, whether those objects are felt, seen, or heard. These response properties are strikingly similar to the properties found in PZ, to which area VIP projects. VIP and PZ do not, however, have identical response properties, as described in the next section. The differences suggest that the two areas are arranged in a hierarchy in which spatial information is more fully processed in PZ.

From sensory input to motor output

Protecting the body requires locating the threat with respect to the body surface, that is, in somatotopic coordinates. Is the object threatening the right forearm, the left side of the face, the forehead? The tactile modality, organized somatotopically, can provide this information for objects that are already touching the body. The auditory modality, anchored to the head, can be used to locate nearby stimuli at least with respect to the head. Visual stimuli, however, are not easily referenced to the body surface. A visual stimulus is first encoded as a location on the retina, but the retina is constantly in motion with respect to the body. In this section we discuss how visual information might be transformed from a spatial coordinate frame centered on the retina to a coordinate frame centered on the body surface that can guide movement.

How do neurons encode the location of visual stimuli? In the retina, a ganglion cell will respond only when light falls on a particular part of the retina, the cell's receptive field. Similar receptive fields, anchored to a location on the retina, are found in cortical areas that are near the retinal input, such as areas V1, V2, MT, V4, and others.

In contrast, in area PZ, many synapses from the retina and only one or two synapses from the motor output, almost none of the visual receptive fields are anchored to the retina. When the eyes move, these visual receptive fields remain stationary. Instead, they 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. These body-part-centered visual receptive fields must require a massive amount of computation to construct. In effect, a neuron in PZ receives input from every part of the retina. Somehow, inputs from different parts of the retina can be turned on and off depending on the position of the eyes, the head, and the arms. How is visual information transformed from the simple retinal receptive fields at the input end to the complex body-part-centered receptive fields found near the motor output?

Area VIP in the parietal lobe may be a crucial intermediate step. As described above, it receives input from retinocentric visual areas such as MT and projects to PZ. Many neurons in VIP have visual receptive fields that are anchored to the retina, moving as the eyes move (Duhamel, Bremmer, BenHamed, & Gref, 1997). About a third of the neurons have visual receptive fields that do not move as the eyes move. These visual receptive fields remain at the same location on a projection screen in front of the monkey even when the monkey is fixating different locations. Many neurons have intermediate properties; they have visual receptive fields that move in the same direction that 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 receptive fields to body-part-centered receptive fields.

Several groups have created neural network models that transform retinal receptive fields into head or arm centered receptive fields (Pouget, Fisher, & Sejnowski, 1993; Salinas & Abbott, 1995; Zipser & Andersen, 1988). 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 about eye position. In order to construct a limb-centered visual receptive field, it is necessary to use additional information about the position of the head on the trunk and the limb with respect to the trunk. (2) When these different types of visual 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.

In summary, we suggest that there is a cortical pathway for locating nearby objects and organizing defensive reactions. This pathway begins in the visual system, where stimuli are located on the retina. This visual information converges with tactile and auditory information in area VIP. In addition to the multisensory convergence in VIP, the visual information also begins to be transformed such that visual stimuli can be located with respect to the body surface rather than on the retina. Finally, in area PZ, this transformation is completed; the neurons respond on the basis of the proximity of objects to specific body parts. The output of area PZ then triggers the appropriate defensive movement.

Area 7b

Multisensory responses similar to those found in PZ and VIP have been reported in other brain areas, including parietal area 7b (Graziano & Gross, 1995; Hyvarinen, 1981; Hyvarinen & Poranen, 1974; Leinonen, Hyvarinen, Nyman, & Linnankoski, 1979; Leinonen & Nyman, 1979; Robinson & Burton, 1980a, 1980b). This area, shown in Figure 27.2, is monosynaptically connected to VIP and PZ and may be part of the same brain system.

We studied single neurons in area 7b in anesthetized monkeys by plotting tactile and visual receptive fields (Graziano, Fernandez, & Gross, 1996; Graziano & Gross, 1995). Tactile stimuli included light touch with a cotton swab, manual palpation, and joint rotation. Visual stimuli included bars and spots of light projected onto a tangent screen, and also objects on the end of a wand, moved by hand in the space near the monkey's body. The objects on a wand were used because most neurons appeared to respond best to real objects rather than to two-dimensional stimuli on a screen. We found a high proportion of bimodal neurons in area 7b, in agreement with previous reports. In at least one part of area 7b, in the upper bank of the lateral sulcus, we found trimodal neurons responding to visual, tactile, and auditory stimuli. Bimodal and trimodal cells had somatosensory receptive fields on the face (13%), the arm (48%), both face and arm (33%), the chest (2%), and the whole upper body (4%). We obtained visual receptive field plots for 50 bimodal cells. Of these, 42% preferred stimuli within 20 cm of the animal, 42% preferred stimuli within 1 meter, and 16% responded well to stimuli at greater distances. When the arm was moved to different locations in front of the monkey, the visual receptive fields did not move with the arm. In no case did we observe an apparent shift of the visual receptive field. These results suggest that the visual receptive fields in 7b, like those in VIP, are not entirely in a coordinate system fixed to the body surface.

The putamen

The putamen is a large subcortical structure that is part of the basal ganglia and appears to play a role in the control of movement. 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 (Alexander, 1987; Crutcher & DeLong, 1984a, 1984b; Kimura, Aosaki, Hu, Ishida, & Watanabe, 1992; Liles, 1985; Schultz & Romo, 1988). We studied the putamen in anesthetized monkeys, testing single neurons for tactile and visual responses (Graziano & Gross, 1993). Tactile stimuli included light touch with a cotton swab, manual palpation, and joint rotation. Visual stimuli included bars and spots of light projected onto a tangent screen, and also objects on the end of a wand, moved by hand in the space near the monkey's body. In the arm and face part of the map, about 25% of the neurons responded to both visual and tactile stimuli. For these bimodal neurons, the visual receptive field was confined to the space near the body, within about 30 cm, and matched 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 was moved to different locations, the visual receptive field also moved, remaining in register with the arm. 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.

Multisensory areas in the human brain

Recent evidence suggests that the human brain contains a set of multisensory areas much like the ones described in this chapter for the monkey brain. In one experiment (Bremmer et al., 2001), subjects in a magnetic resonance imaging (MRI) scanner were exposed to tactile, visual, and auditory stimuli in separate trials. A small set of cortical areas appeared to be multisensory; that is, they could be activated above baseline by any of the three sensory modalities. One of the multisensory areas was located in the parietal lobe, on the floor of the intraparietal sulcus, closely matching the location of area VIP in the monkey brain. A second multisensory 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 multisensory 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 multisensory 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 subjects in an MRI scanner made judgments 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 contains a set of multisensory cortical areas, many of which match the location of the multisensory areas in the monkey brain. It will be important to ascertain whether these areas in the human brain are engaged during tasks that tap into a defensive or flinch mechanism.

Summary

In this chapter we described a specific system of brain areas that are multisensory; they combine vision, audition, and touch. Neurons in these multisensory areas encode the location and movement of objects that are in the space near the body, within about 30 cm. Electrical stimulation experiments suggest that this particular set of multisensory areas serves the purpose of defending the body against nearby, threatening objects. In this view, objects that enter the space near the body will activate neurons in this system of areas, and these neurons will in turn induce the appropriate flinch or defensive movement. This system might serve as a model for understanding how sensory information is transformed by the brain into motor output.

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