

Mapping Space With Neurons

M.S.A. Graziano and C.G. Gross

The left fielder squints at the baseball as it curves toward him. He adjusts his hand and body, and the ball lands in his mitt. Somehow, the changing pattern of light on his retina was transformed into a motor command that brought his hand to the correct location for catching the ball. How was this accomplished? Is there a map of visual space in the brain that encodes the location of the ball and the fielder's glove? In this article, we review some recent experiments, using monkeys, on visuomotor transformations in the brain. We ask how neurons represent the location of a stimulus for the purposes of looking at it, reaching toward it, or avoiding it.

A DISTRIBUTED REPRESENTATION OF SPACE IN PARIETAL CORTEX

On the basis of neuropsychological research over the past 50 years,¹ we would expect that damage to the fielder's posterior parietal cortex would disrupt his ability to notice, localize, and reach toward the ball, as well as related visuospatial abilities such as finding his way to the ball field and imagining the billboards around the field. He should still be able to read the scoreboard and throw a ball, but his sense of visual space should be seriously dis-

Michael S.A. Graziano is a doctoral candidate and **Charles G. Gross** a Professor of Psychology, both at Princeton University. Address correspondence to Michael Graziano, Department of Psychology, Princeton University, Princeton, NJ 08544; e-mail: graziano@phoenix.princeton.edu.

turbed. How do the neurons in posterior parietal cortex provide this sense of visual space?

In general, a sensory neuron locates stimuli by means of its receptive field. A visual neuron responds when a stimulus falls on a particular part of the retina, the neuron's visual receptive field. That is, the neuron reacts only if the stimulus is at a particular *retinal coordinate*. A set of such cells with receptive fields scattered across the retina forms a *retinal coordinate system*, specifying the location of the image on the retina. As the eyes move, the receptive fields also move, and thus the entire coordinate system moves. This type of receptive field, which is "fixed" to the retina, is found in most visual areas of the brain, such as V1 or striate cortex.

Andersen and his colleagues¹ have been studying a more complex type of visual neuron, in a region of the posterior parietal cortex known as area 7a (see Fig. 1). These cells have rather unusual properties that may help explain the crucial role of the parietal cortex in the perception of space. What is different about

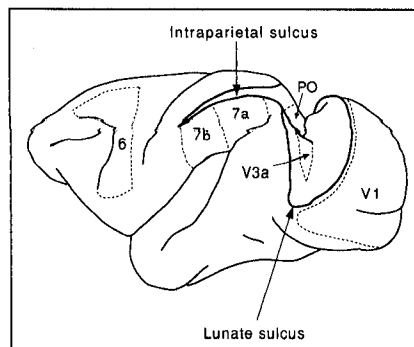


Fig. 1. Lateral view of the left hemisphere of a macaque cerebral cortex showing some of the areas involved in the processing of visual space. Dotted lines indicate the borders of areas. The intraparietal and lunate sulci have been opened up to show the buried cortex.

these cells is that their activity depends not only on the location of the stimulus on the retina, but also on the position of the eye in the orbit. For example, the responses of some neurons increase as the eyes look toward the left; the responses of other neurons increase or decrease as the eyes look in other directions. This change in response magnitude occurs even if an identical stimulus is presented to the same part of the retina. Zipser and Andersen have shown that a set of such cells contains enough information to locate a visual stimulus with respect to the head, that is, to represent visual space in *head-centered coordinates*. This spatial information is coded by the pattern of activity across a population of area 7a neurons. By contrast, the activity of a single 7a neuron, considered by itself, carries virtually no information about stimulus location in space, but only about stimulus location on the retina. Recently, cells with similar properties have been found in another visual area, area V3a, which lies in the junction of the parietal and occipital lobes² (see Fig. 1).

A BIMODAL REPRESENTATION OF SPACE IN PREMOTOR CORTEX

One of the main outputs of the parietal lobe is to the premotor cortex, or area 6, which lies in the frontal lobe (Fig. 1). Most neurons in area 6 respond to touch on the skin or to rotation of the joints; that is, they have somatosensory receptive fields. These receptive fields are arranged to form a topographic map of the body, similar to the homunculus ("simunculus") in somatosensory cortex. Rizzolatti and his colleagues³ have shown, and we have confirmed,⁴ that in the lower part of area 6, cells with tactile receptive fields on the face or arms also respond to visual stimuli: They are bi-

modal, sensitive to both sight and touch. Furthermore, the visual and tactile fields correspond spatially: For each cell, the visual receptive field extends from the tactile field, outward from the body, into nearby space (see Fig. 2). When a visual stimulus approaches within about 20 cm of the tactile receptive field, it enters the visual receptive field, and the cell fires. As first suggested by Rizzolatti and his colleagues, this spatial correspondence between the visual and tactile receptive fields could play a role in localizing visual stimuli near the body. He supported this view by showing that lesions of ventral area 6 impair the ability to localize stimuli near the face, but leave intact the ability to localize stimuli that are beyond reaching distance.

In marked contrast to the receptive fields in most visual areas, including parietal area 7a, the visual receptive fields in area 6 do not move when the animal's eyes move. Rizzolatti has suggested that these visual receptive fields are fixed to the head rather than the eyes. If this were true, then the receptive fields would move as the head moves. Such a receptive field would directly measure the location of a stimulus in head-centered coordinates, rather than in retinal ones. However, in Rizzolatti's experiments, the effect of head movement on the receptive

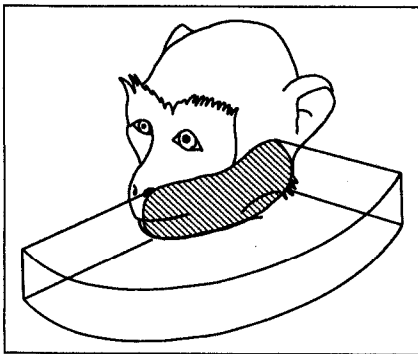


Fig. 2. Tactile receptive field (striped) and visual receptive field (boxed) of a bimodal cell in the putamen.⁴ Similar bimodal receptive fields have been found in areas 6 and 7b.

fields was not studied because the animal's head was held in place. The receptive fields could have been attached to the trunk instead of the head or, for that matter, to the arm, the foot, or even the floor of the room. The results show only that they were not fixed to the retina.⁵ As described in the next section, the representation of visual space may be more complex than a strictly head-centered one.

A SYSTEM OF BIMODAL AREAS FOR CODING SPACE

In our lab, we have been studying the representation of space in parietal area 7b, premotor area 6, and the putamen, a large subcortical nucleus forming part of the basal ganglia.⁴ All three areas are directly interconnected, and we believe that they contain a system for representing visual space near the body. Area 7b and the putamen have bimodal, visual-tactile properties virtually identical to those just described for area 6. For these bimodal cells, the visual receptive field matches the location of the tactile receptive field, and is confined in depth to a region near the animal (see Fig. 2). Because the tactile fields are arranged in a map of the body surface, the associated visual receptive fields form a map of the immediate space around the body.

For many of the neurons with tactile receptive fields on the arm or the hand, when we placed the arm in different locations, the visual receptive fields moved along with it (see Fig. 3). For example, moving the arm leftward also moved the visual receptive field leftward by the same amount. When the arm was bent back out of the animal's sight, the cell usually ceased or markedly reduced its response to visual stimuli, presumably because the visually responsive region surrounding the arm was no longer within the monkey's view. In the putamen, 20% of the

bimodal arm cells showed this dynamic property, and in area 6, 67% did. In area 7b, however, none of the visual responses depended on the position of the arm. Perhaps area 7b is an earlier processing stage with simpler properties.

Visual receptive fields that are fixed to the arm are ideally suited to locate a stimulus with respect to the arm, that is, in arm-centered coordinates, not retinal or head-centered ones. More generally, we predict that the putamen and inferior area 6 encode stimuli in a body-part-centered fashion. According to this hypothesis, bimodal cells with tactile receptive fields on the face should have visual receptive fields that are attached to the head and move as the head moves, and the small proportion of bimodal cells with tactile receptive fields on the chest should have visual receptive fields that are fixed to the trunk and move only when the trunk moves. We expect that other parts of the body have receptive fields attached to them as well. Thus, the visual space near the animal would be represented as if it were a gelatinous mold surrounding the body, deforming whenever the head rotates or the limbs move. Such a map would give the location of a visual stimulus with respect to the nearest body part, in somatotopic coordinates.

THE SUPERIOR COLLICULUS AND MULTIMODAL SPACE

Visual receptive fields in area 6 and the putamen that move with the arm require considerable neural computation. They must integrate visual information from the retina with information about the position of the eye, the head, the shoulder, and the elbow. The optic tectum, a phylogenetically old structure in the midbrain, carries out a similar cross-modal integration. It plays a major role in encoding the locations of sensory stimuli in different modali-

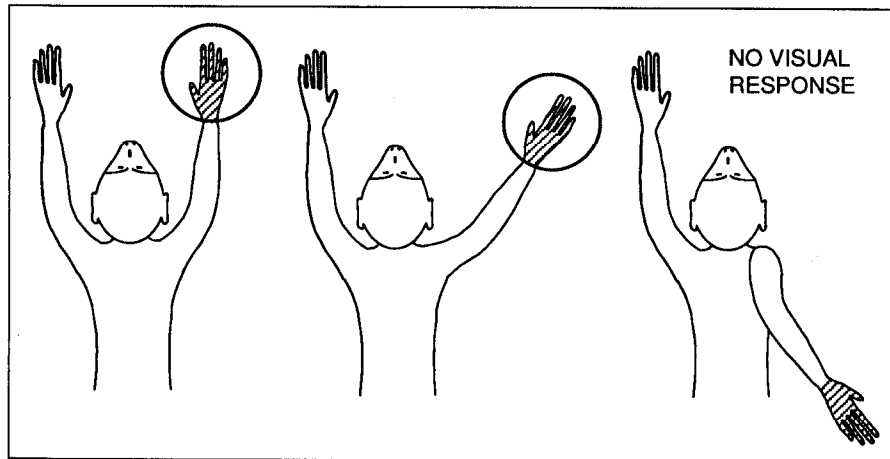


Fig. 3. A bimodal cell from the putamen with a tactile receptive field (striped) on the hand and a visual receptive field (circled) extending 5 cm from the hand. When the arm moved, the visual receptive field moved with it. When the arm was bent out of sight, the visual response disappeared.⁴

ties and coordinating orienting responses toward them. In primates, where it is known as the superior colliculus, it is specialized for programming saccadic (i.e., rapid and ballistic) eye movements.⁶

Neurons in the deep layers of the superior colliculus respond to visual, auditory, and tactile stimuli. Many of these neurons are multimodal, and in these cases the receptive fields for the different sensory modalities correspond spatially. For example, a bimodal, visual-auditory cell that responds to visual stimuli above and to the left of the animal would also respond to a sound coming from the upper left. Furthermore, the receptive fields are organized topographically, so there is a somatosensory map, a visual map, and an auditory map of space, all in register with each other.⁷

Sparks and his associates have demonstrated some remarkable properties of these colliculus cells.⁸ In one experiment, the monkey was required to remember the location of a visual stimulus that had just been turned off. Even though the stimulus was no longer present, colliculus cells continued to fire. They appeared to be "remembering" the location of the stimulus. If the animal then moved its eyes, aligning a different part of the retina with the re-

membered location, cells with receptive fields at the new retinal coordinates became active, even though the stimulus was no longer present and had never directly stimulated that portion of the retina. That is, the colliculus behaved as if the stimulus were still visible, and extrapolated where the image would have fallen on the retina.

In another experiment, Jay and Sparks recorded from colliculus neurons that had auditory receptive fields. Because the ears are fixed to the head, an auditory receptive field might have been expected to be fixed with respect to the head. However, when the monkey moved its eyes to different locations, the auditory receptive fields moved along with the eyes, remaining fixed to the retina. Again, the colliculus was behaving as if the stimulus were visible, and calculating its retinal location.

These experiments clarify how the colliculus encodes the spatial locations of visual, remembered, and auditory targets. It calculates the region on the retina that is aligned with the target, and all cells with receptive fields at that retinal location respond to the target. This result is particularly intriguing in the case of auditory and remembered stimuli because they do not stimulate the

retina directly. This phenomenon is similar to the arm-centered visual responses in area 6 and the putamen, described in the previous section. In both cases, the sensory receptive fields are fixed to a particular body part, and move as that body part moves. In the case of the colliculus, the receptive fields are fixed to the eye. In the case of the putamen and area 6, the receptive fields are fixed to the arm. The neuronal computations involved in producing these complex and dynamic response properties may be very similar in the different brain areas.

FROM SENSORY SPACE TO MOTOR SPACE

The retinal coordinates encoded in the colliculus are particularly well suited for making saccadic eye movements. If the location of a stimulus is encoded as 10° left of the fovea, for example, the same code can be fed directly into the motor system, directing the eyes to move 10° to the left. Indeed, superior colliculus neurons have both sensory and motor functions. When a stimulus falls in the receptive field, it causes the cell to fire. If the animal then chooses to fixate the stimulus, the same cell will fire immediately before the eye movement, driving the eye to the correct location. Thus, the superior colliculus is a sensorimotor interface, where the location of the stimulus is encoded in the same coordinate system used for guiding the response.

In a similar fashion, the arm-centered visual responses in the putamen and in area 6 are ideally suited to guide reaching toward an object, because they give the direction that the arm must move in order to do so. Indeed, neurons in both the putamen and area 6 have motor responses as well as sensory ones, and like neurons in the colliculus appear to function as sensorimotor interfaces. For example, many neurons

in area 6 respond when the monkey reaches toward a target. These neurons are spatially tuned: They respond best when the arm reaches into a particular region of space. Furthermore, this "motor field" moves as the arm moves, rotating at roughly the same angle that the shoulder has rotated.⁹ That is, the motor response fields for arm movements appear to be arm centered, just as some of the visual receptive fields near the arm are. In support of this view, psychophysical evidence from humans shows that reaching is done in an arm- or shoulder-centered coordinate system.¹⁰

Retinal and arm-centered coordinate systems are not the only useful arrangements. When President Clinton reaches toward a hamburger with his mouth, he must encode the spatial relationship between his mouth and the target, in "mouth centered" coordinates. Bimodal neurons in area 6 with both tactile receptive fields near the mouth and visual receptive fields in the space around the mouth may help serve this purpose. When a soccer player heads a ball, he must encode the changing relationship between the ball and his head. Visual receptive fields attached to the forehead would be useful in this condition.

When he elbows a fellow player in the ribs, "elbow centered" receptive fields would be helpful, too. Indeed, it would be useful to have visual receptive fields fixed to various parts of the body surface, for the purpose of hitting, grasping, or avoiding visual stimuli near these body parts. We hypothesize that the bimodal portions of the brain provide exactly such a "body part" representation of space.

In summary, visual space appears to be represented in a modular fashion. There are multiple representations of space in the brain, and each one is dedicated to a specific purpose in the motor system. In each case, the visual receptive fields, and therefore the spatial coordinate system, may be attached to the relevant body part. The highest levels of spatial processing are not, strictly speaking, in the visual system itself, but in visuomotor areas such as the putamen, area 6, and the superior colliculus.

Acknowledgments—This research was supported by Grant MH 19420 from the National Institutes of Health and Grant 93-330 from the National Aeronautics and Space Administration. We would like to thank Hillary Rodman, Allen Repp, and C.R. Gallistel for their helpful comments on an earlier draft.

Notes

1. R.A. Andersen, Visual and eye movement functions of the posterior parietal cortex, *Annual Review of Neuroscience*, 12, 377-403 (1989).
2. C. Galletti and P.P. Battaglini, Gaze dependent visual neurons in area V3A of monkey prestriate cortex, *Journal of Neuroscience*, 9, 1112-1125 (1989).
3. G. Rizzolatti and A. Berti, Neglect as a neural representation deficit, *Review of Neurology (Paris)*, 146, 626-634 (1990); L. Fogassi, V. Gallese, G. di Pellegrino, L. Fadiga, M. Gentilucci, G. Lupino, M. Matelli, A. Pedotti, and G. Rizzolatti, Space coding by premotor cortex, *Experimental Brain Research*, 89, 686-690 (1992).
4. M.S. Graziano and C.G. Gross, A bimodal map of space: Tactile receptive fields in the macaque putamen with corresponding visual receptive fields, *Experimental Brain Research*, 97, 96-109 (1993); M.S. Graziano and C.G. Gross, The representation of extrapersonal space: A possible role for bimodal, visual-tactile neurons, in *The Cognitive Neurosciences*, M.S. Gazzaniga, Ed. (MIT Press, Cambridge, MA, 1994).
5. Similar cells were reported in area PO of the parietal lobe by C. Galletti, P.P. Battaglini, and P. Fattori, Parietal neurons encoding spatial locations in craniotopic coordinates, *Experimental Brain Research*, 96, 221-229 (1993).
6. P.H. Schiller, The superior colliculus and visual function, in *The Handbook of Physiology*, Sec. 1, Vol. III, I. Darian-Smith, Ed. (American Physiological Society, Bethesda, MD, 1984).
7. B.E. Stein and M.A. Meredith, *The Merging of the Senses* (MIT Press, Cambridge, MA, 1993).
8. D.L. Sparks, The neural encoding of the location of targets for saccadic eye movements, in *Brain and Space*, J. Paillard, Ed. (Oxford University Press, New York, 1991).
9. R. Caminiti, P.B. Johnson, and A. Urbano, Making arm movements within different parts of space: Dynamic aspects in the primate motor cortex, *Journal of Neuroscience*, 10, 2039-2058 (1990).
10. J.F. Soechting and M. Flanders, Sensorimotor representations for pointing to targets in three-dimensional space, *Journal of Neurophysiology*, 62, 582-594 (1989); J.F. Soechting and M. Flanders, Errors in pointing are due to approximations in sensorimotor transformations, *Journal of Neurophysiology*, 62, 595-608 (1989).