In: J.King, and K.H. Pribram (Eds.), Scale Conscious Experience: Is the Brain Too Important To Be Left to Specialists to Study?, Lawrence Erlbaum, Mahwah, NJ, 1995.

201

From Eye to Hand

Michael S. A. Graziano and C. G. Gross
Princeton University
Green Hall, Princeton, NJ, 08544

How are we able to reach accurately toward objects near us and avoid ones that are approaching, even though the objects and our own eyes, head, limbs and body may be continually changing positions? How does the brain construct a representation of the visual space surrounding the body, and how does this representation guide movement?

The broad outline of the transformation of vision into action has been known for some time from anatomical, physiological, neuropsychological and neuropathological studies, in monkeys and humans [e.g. 18, 20, 27, 37, 52]. Information from the retina about motion and space passes primarily, although not exclusively, through the magnocellular portion of the lateral geniculate nucleus and then to primary visual cortex (V1). The information is further processed by extrastriate visual areas in the "dorsal stream". It is unclear whether these areas actually form one or more processing streams or, alternatively, a parallel distributed network. Among the areas in the Macaque monkey that are thought to be important for spatial functions are V2, V3A, and PO, and for functions involving moving stimuli, MT, MST, and STP. These areas in turn project to several subdivisions of the posterior parietal cortex. (See Figure 1).

In addition to its visual input, posterior parietal cortex also receives tactile, joint, efferent-copy, auditory, and vestibular input [for review see 3, 51]. Because of its multimodal nature, this cortical region is ideally suited to process the space surrounding the body. Posterior parietal cortex projects to a variety of areas involved in the further processing of visual space and visuo-motor coordination. These areas include the hippocampus, the lateral prefrontal cortex, the frontal eye fields, the supplementary eye fields, the superior colliculus, the ventral premotor cortex, the supplementary motor area, and the striatum [10, 26, 30, 34, 40, 45, 49, 51, 52]. Some of these areas, in turn, modulate the activity of motor structures such as primary motor cortex, the red nucleus, the spinal cord, and eye movement generators in the brain stem [e.g., 2, 24, 37, 45, 52]. Thus, light falling on the retina can eventually result in motor behaviour.

A major puzzle in this processing sequence lies in the territory between the clearly visual and the clearly motor. How are the retinal coordinates of the first stages of visual processing translated into the joint coordinates of the motor system? The answer would seem to lie primarily in posterior parietal cortex and structures efferent to it. In this paper we discuss some of these areas and how they represent visual and visuo-motor space. Emphasis is on the parietal cortex and on two areas recently implicated in visuo-spatial functions, namely, the putamen (part of the basal ganglia) and premotor cortex.

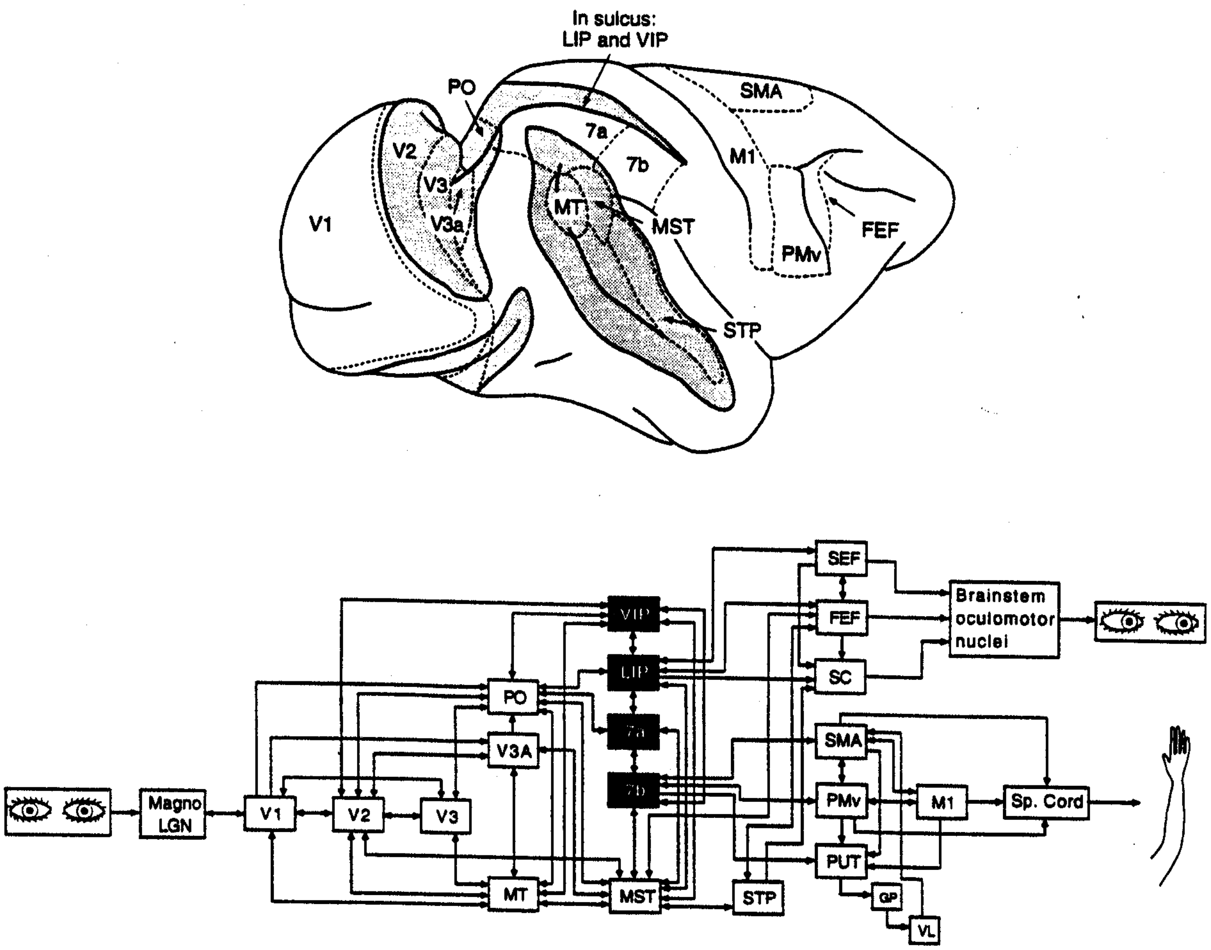

Figure 1: Top. Lateral view of macaque cerebral cortex showing some of the cortical areas involved in the representation of visual space and visuomotor coordination. Major posterior sulci have been "opened up" to show the buried cortex in grey. Bottom. Some of the neuronal pathways by which visual information entering the eye might guide movement of the eyes and limbs. Areas shown in black are in the posterior parietal lobe. SEF, supplementary eye fields; FEF, frontal eye fields; SC, superior colliculus; SMA, supplementary motor area; PMv, ventral premotor cortex; PUT, putamen; GP, globus pallidus; VL, ventrolateral thalamus; STP, superior temporal polysensory area.

THEORIES OF SPACE CODING IN POSTERIOR PARIETAL CORTEX

Lesions to the posterior parietal cortex in humans and monkeys cause devastating visuo-spatial and visuo-motor imparements. The symptoms can include deficits in reaching and pointing to visual targets, avoiding obstacles, learning and remembering routes, judging distance and size, recognizing spatial relations, fixating a target, following a moving stimulus, localizating a touch on the body, and attending to the contralateral side of space [e.g., 6, 7, 8, 17, 25, 33, 36]. By contrast, object recognition ability and other cognitive functions can be essentially normal. How do neurons in parietal cortex subserve these spatial functions?

There is no evidence for a topographic map of space in parietal cortex [3, 42, 50], not even for a map of the retina such as is found in lower-order visual areas. In any case, as Sir Gordon Holmes pointed out long ago [36], in order to calculate the spatial location of an object it is not enough to know where the visual image falls on the retina. It is also necessary to know where the eyes are pointing, how the head is angled, and where the body is located. Andersen and his colleagues have found neurons in monkey parietal areas 7a and LIP which combine exactly these signals [5]. The firing rate of these neurons is a function of the position of the stimulus on the retina, the position of the eyes in the orbit, and the angle of the head on the trunk. Some 7a neurons are also modulated by vestibular information about the orientation of the body in space. Andersen et al. have suggested that these neurons provide a spatial coordinate system that can locate visual stimuli. However, whether this coordinate system is centered on the head, the trunk, or the external environment is not clear. Each of these possibilities has been proposed at different times, and all are consistent with the data [3, 5, 9, 53].

Galletti et al. [22] have proposed a different solution for the role of posterior parietal cortex in spatial cognition. They studied visually responsive cells in area PO, in the parieto-occipital sulcus, and found that for a small percentage of cells, the visual receptive fields did not move when the eyes moved. Instead, these receptive fields remained anchored to one location in space. The firing of one of these cells would therefore signal the presence of a stimulus at that particular spatial location. The investigators concluded that these visual receptive fields must be fixed with respect to the head, coding space in head-centered coordinates. However, they did not test the crucial prediction of their idea: namely, that their putative head-centered receptive fields would move when the head was rotated. Thus, although these receptive fields did not move with the eyes and therefore were not in a coordinate system centered on the retina, they might have been in a coordinate system centered on the chest, the arm, the leg, or some external landmark. There is no evidence that they were centered on the head.

Duhamel et al. [19] have proposed yet another function for posterior parietal cortex. In their view, parietal cortex, particularly area LIP, does not encode external space at all. Instead, it encodes the locations of visual images on the retina, and helps to guide movements of the eye. In this way, a visual image of interest can be shifted onto the fovea. The proprioceptive, efferent-copy, and vestibular information present in parietal cortex, according to this view, is used to predict how the visual image will shift across the retina as a result of head and eye movements.

Why has the nature of spatial processing in the posterior parietal cortex been so elusive? One reason has been the belief that parietal cortex must be the endpoint of spatial processing, and that it contains one central representation and one coordinate system. This monolithic view of space coding is unlikely to be correct, since posterior parietal cortex consists of a large number of sub-regions [14], and these sub-regions project to a variety of other brain structures many of which are known to process visual space. We suggest that posterior parietal cortex is an intermediate stage in the processing of space, for which there is no single coordinate system, and for which visual space has not yet been represented in the form of a topographic map [30, 34]. On this view, projections from parietal cortex distribute this implicit, partially processed spatial information to other areas, which construct their own, special purpose maps, variously head-centered, gaze-centered, trunk-centered, or allocentric. The following sections describe two of these target areas, the putamen and the ventral premotor cortex. Unlike posterior parietal cortex, each of these areas contains a topographic map of visual-motor space. Also unlike parietal cortex, the visual receptive fields in these areas are organized in specific coordinate systems.

CODING OF SPACE IN THE PUTAMEN

Most putamen neurons respond to a touch on the skin, rotation of the joints, or deep muscle pressure, and many will respond only when the animal makes a voluntary movement [e.g., 1, 15, 16, 38]. These somatosensory and motor fields are organized topographically; the legs are represented in the dorsal part of the putamen, the trunk and arms in the central part, and the face in the ventral part. Because of its physiological properties and interconnections with primary somatosensory and motor cortex, the putamen has been considered largely a somatomotor structure [2]. However, it also receives direct projections from visual areas of the parietal lobe [13]. We recorded from the putamen both in anesthetized and awake macaque monkeys, and found visual responses in the face and arm region of the somatotopic map [28, 31]. Visual and tactile responses were often combined in a single neuron, and for these bimodal neurons, the location of the visual receptive field usually matched the location of the tactile receptive field. Because the tactile receptive fields were arranged to form a map of the body surface, the visual receptive fields, attached to the tactile fields, therefore formed a map of the visual space immediately surrounding the body.

A typical example of a bimodal cell is shown in Figure 2. The tactile receptive field, located on the cheek, was plotted while the animal's eyes were covered. When the eyes were uncovered, the cell responded to visual stimuli placed within about 10 cm of the cheek. We also found bimodal cells with tactile responses on the arm and the hand, as shown in Figure 3. The three dimensional extent of these visual receptive fields was similar under monocular and binocular viewing conditions, and therefore the cells must have been utilizing monocular cues for depth.

Figure 4 shows the relative proportions of different categories of cells found in the putamen, both in anesthetized and in awake monkeys. In anesthetized monkeys, of the 354 neurons studied, 40% were somatosensory, 12% were visual, 24% were bimodal visual-somatosensory, and 23% were unresponsive under our testing conditions. In awake monkeys, we also found neuronal activity that was related to voluntary movement. Of 35 neurons studied, 23% had motor-related activity, 17% were somatosensory, 9% were visual, 17% were bimodal visual-somatosensory, and 34% were unresponsive.

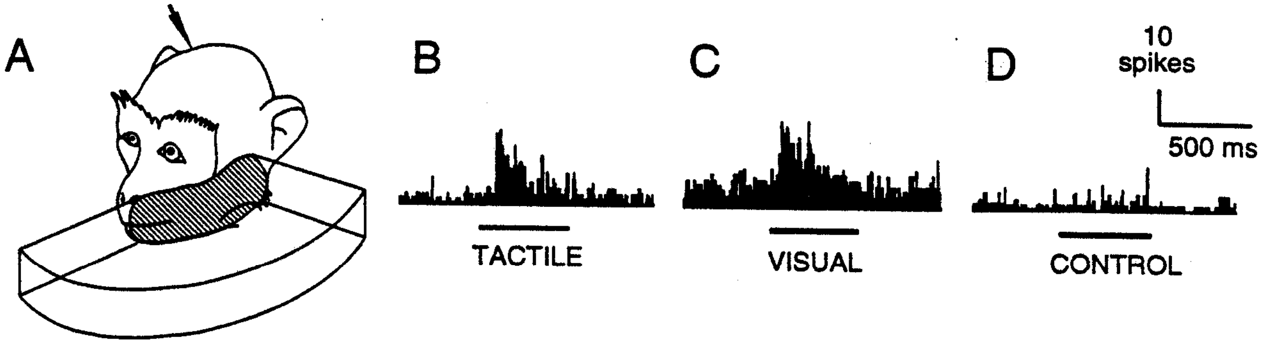

Figure 2: Peri-stimulus time histograms, summed over 10 trials, for a typical bimodal putamen cell. A. The tactile receptive field (stippled) and the visual receptive field (boxed) are in register. The arrow indicates the hemisphere recorded from. B. Response to touching the face with the eyes covered. C. Response to a stimulus approaching the face within 10 cm with the eyes open. Background activity increased when the eyes were uncovered, even before the stimulus (underline) was presented. D. Same as C but with the eyes covered [28].

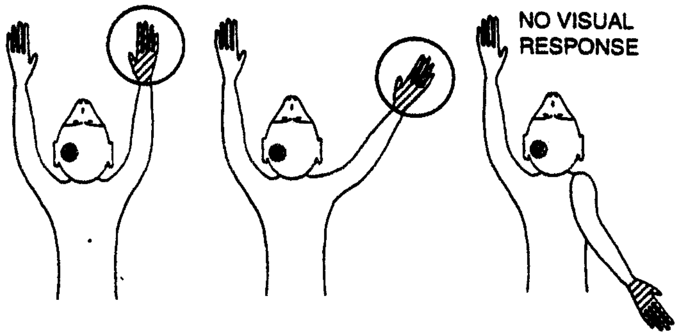

Figure 3: Tactile receptive field (shaded) and visual receptive field (circled) for a bimodal cell in the putamen of an anesthetized monkey. When the arm was moved to different locations, the visual receptive field moved with it, remaining in register with the tactile field on the hand. When the tactile field was placed out of view, the cell did not respond to visual stimuli. The black dot indicates the hemisphere recorded from [28].

The bimodal neurons in the putamen are well suited to encode the locations of visual stimuli within reaching distance of the body. Since the visual receptive fields are generally large, each one provides only relatively crude information about stimulus location. However, a population of overlapping receptive fields could localize stimuli precisely. Even the distance from the animal to the stimulus could be encoded precisely, since different cells have receptive fields that extend to different depths. Why should the putamen contain such a map of visual space? The putamen is a motor structure, and a high proportion of its neurons respond during voluntary movement [e.g., 1, 16]. One possibility, therefore, is that these bimodal cells function to locate visual stimuli for the purpose of making movements toward or away from them.

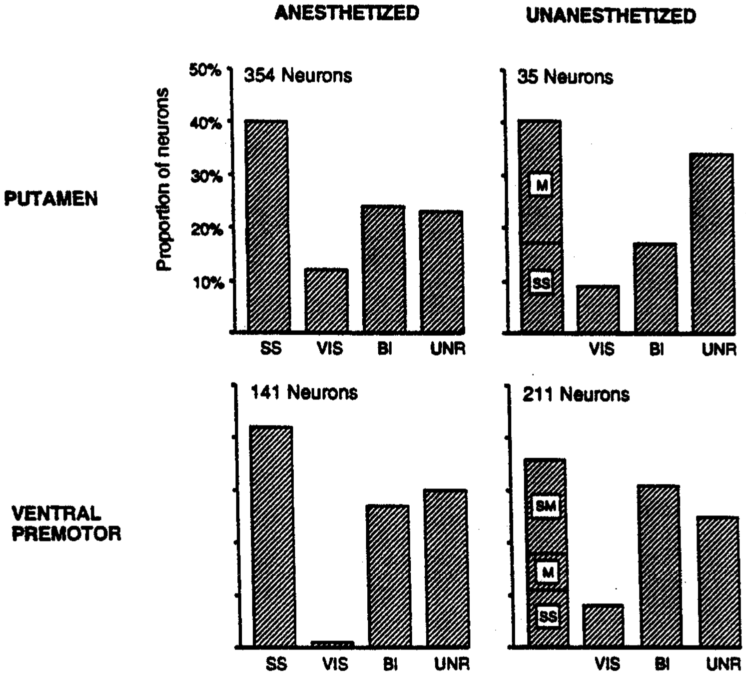

Figure 4: Proportions of somatosensory (SS), visual (VIS), bimodal (BI), unresponsive (UNR), motor (M), and both somatosensory and motor (SM) cells in the putamen and PMv of anesthetized and awake monkeys [31].

CODING OF SPACE IN VENTRAL PREMOTOR CORTEX

As in the putamen, neurons in the ventral premotor cortex (PMv) respond to somatosensory stimuli and are active during voluntary movement [e.g., 11, 23, 43, 52]. The lateral part of PMv contains a somatosensory and motor representation of the face, and the medial part contains a representation of the arms [23, 43]. As first shown by Rizzolatti et al. [44], and subsequently corroborated by our own studies [31, 32], many of the somatosensory cells in PMv also respond to visual stimuli. That is, PMv contains bimodal, visual-tactile cells. These cells have similar properties to the bimodal cells in the putamen. Furthermore, as shown in Figure 4, the proportions of cell types are also very similar between the putamen and PMv. PMv projects to the putamen, and both receive their visual input from the same regions of the parietal lobe [12, 39, 41].

Fogassi, Rizzolatti and colleagues [21] found that the visual receptive fields of most PMv cells did not move when the monkey moved its eyes. Rather, the receptive fields seemed to be stationary in space. On this basis the investigators suggested that the receptive fields were fixed to the head, or possibly the trunk, and therefore coded space in head- or trunk-centered coordinates rather than in coordinates centered on the retina. However, this idea remained untested because the investigators did not study the effect of head and trunk movement. Head-centered visual receptive fields should move when the head is roated, and trunk-centered receptive fields should move with the trunk.

In order to clarify the nature of the visual coordinate system used by PMv, we tested PMv cells while manipulating the positions of various body parts including the arm, the head, and the eyes [32]. For bimodal cells with a tactile response on the arm or the hand, we tested the effect of moving the arm to different positions. Figure 5 shows an example of a cell studied in an anesthetized monkey whose eyes were focused straight ahead. The tactile receptive field covered the contralateral arm. When the arm was placed in different locations, the visual receptive field also changed location, remaining in rough register with the arm. Clearly, this visual receptive field was not fixed to one site on the retina; that is, it was not retinocentric. But it was also not head- or trunk-centered, as had been proposed by Rizzolatti and colleagues. Instead, it was arm-centered, encoding the locations of visual stimuli with respect to the arm. Most bimodal PMv cells with tactile responses on the arm (88% of 42 cells tested) had similar, arm-centered visual receptive fields. (A few cells tested in the putamen showed the same arm-centered behaviour. See Figure 3).

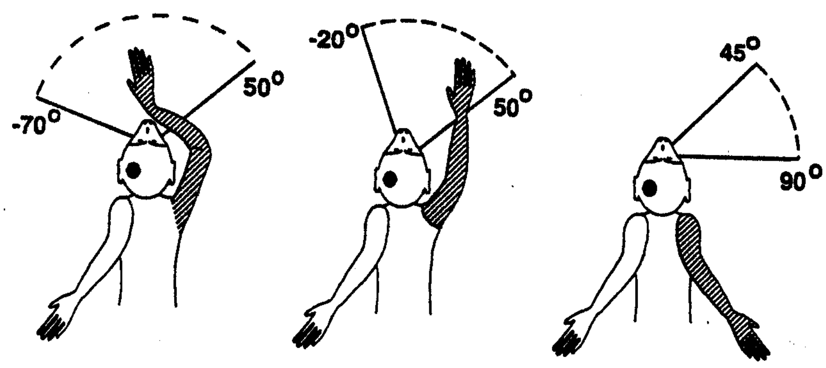

Figure 5: Tactile receptive field (shaded) and visual receptive field (solid lines) for a bimodal cell in PMv of an anesthetized monkey. When the arm was moved to different locations, the visual receptive field moved with it, remaining in approximate register with the tactile field on the arm. The black dot indicates the hemisphere recorded from [32].

Figure 6 (left) shows the paradigm that we used to test the effect of eye position and arm position in awake monkeys [32]. The visual receptive field was plotted by means of a ping-pong ball that was mounted on a robot arm and advanced toward the monkey along various trajectories. In general, PMv cells responded vigerously as the ping-pong ball entered their visual receptive fields. The effect of eye position was studied by requiring the monkey to fixate on one of three lights, A, B or C, spaced 20° apart along the horizontal meridian. The effect of arm position was studied by testing the cell while the arm was strapped in one position, and then strapping the arm into a new position and testing the cell again.

Figure 6 (right) shows the result for a neuron with a tactile receptive field on the contralateral arm. The visual response remained at the same location near the arm, whether the eyes fixated on light A, light B, or light C. That is, even a 40° shift in eye position failed to change the location of the visual receptive field. However, when the arm was bent toward the left, the visual response moved with the arm. Therefore, this visual receptive field was centered on the arm, not on the retina.

For cells with a tactile response on the face, such as the one illustrated in Figure 7, we tested the effect of rotating the head to the right or the left by 15 degrees, and found that in most cases (95% of 20 cells tested) the visual receptive fields moved with the head. By contrast, when we placed the arm in different locations or required the animal to look in different directions, the visual receptive fields remained stationary, fixed with respect to the head. Therefore, these receptive fields associated with the head are indeed in head-centered coordinates.

Our results indicate that PMv and possibly the putamen use more than one visual coordinate system. Cells related to the arm use arm-centered coordinates, locating visual stimuli with respect to the arm; and cells related to the face use head-centered coordinates, locating stimuli with respect to the head. Perhaps other body parts such as the legs or trunk also have associated visual coordinate systems. What function might such a "body-part-centered" representation of space serve? Arm-centered neurons would be useful for hand-eye coordination, guiding the arm toward or away from visual targets. Indeed, a high proportion of neurons in the putamen and PMv are active during reaching [e.g., 1, 11, 16, 38, 52]. In PMv, the cells are spatially tuned, responding best when the arm reaches into a particular region of space [11]. When the starting position of the arm is changed, this motor field also moves, maintaining the same spatial relationship with the arm. That is, just as for the visual receptive fields, the motor response fields are arm-centered. These neurons would therefore appear to form a sensory-motor interface, encoding the location of the target in the same spatial coordinate system that is used to control the arm.

By extension, head-centered visual receptive fields would be useful for visuo-motor coordination of the head, such as for reaching with the mouth toward food or enemies, flinching from approaching objects, heading soccer balls, or kissing accurately. Indeed, it would be useful to have a visual coordinate frame fixed to each part of the body surface, for the purpose of hitting, grasping, or avoiding visual stimuli in the space near that body part. We hypothesize that PMv and the putamen provide exactly this type of visual map [29, 34, 35].

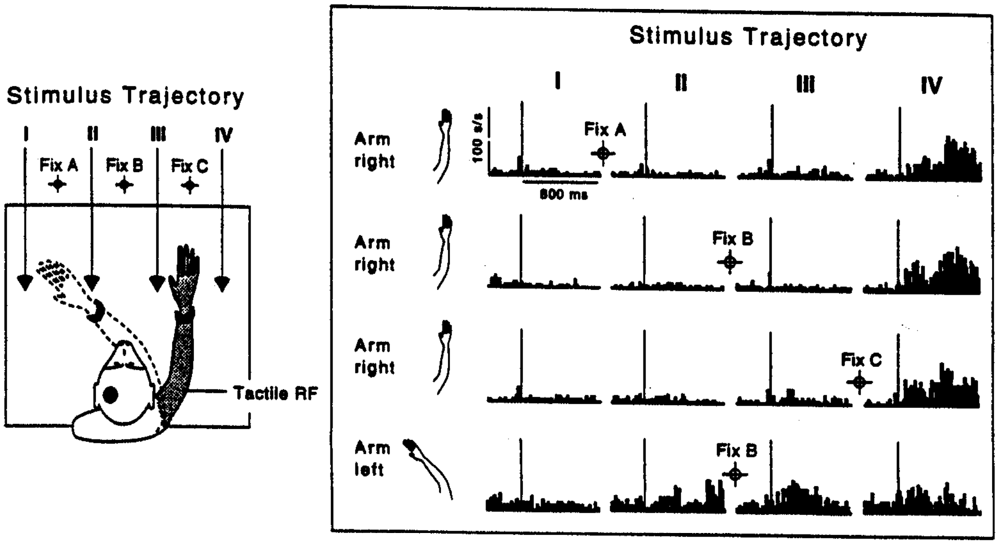

Figure 6: Left. Experimental paradigm for testing cells with receptive fields on the arm. On each trial the animal fixated one of three lights 20° apart (A, B or C) and the stimulus was advanced along one of four trajectories (I-IV). The arm contralateral to the recording electrode was either fixed straight ahead or bent leftward across the chest. The stippling shows the tactile receptive field of the cell illustrated on the right. Right. Histograms of neuronal activity, summed over 10 trials, as a function of eye position (A, B, C), stimulus position (I-IV), and arm position (right or left). The vertical lines indicate stimulus onset. When the arm was fixed to the right, the neuron responded best to the right-most stimulus trajectory (IV), whether the eye looked to the left (A), to the center (B), or to the right (C). When the arm was bent leftward across the chest, the visual receptive field also extended across the chest.

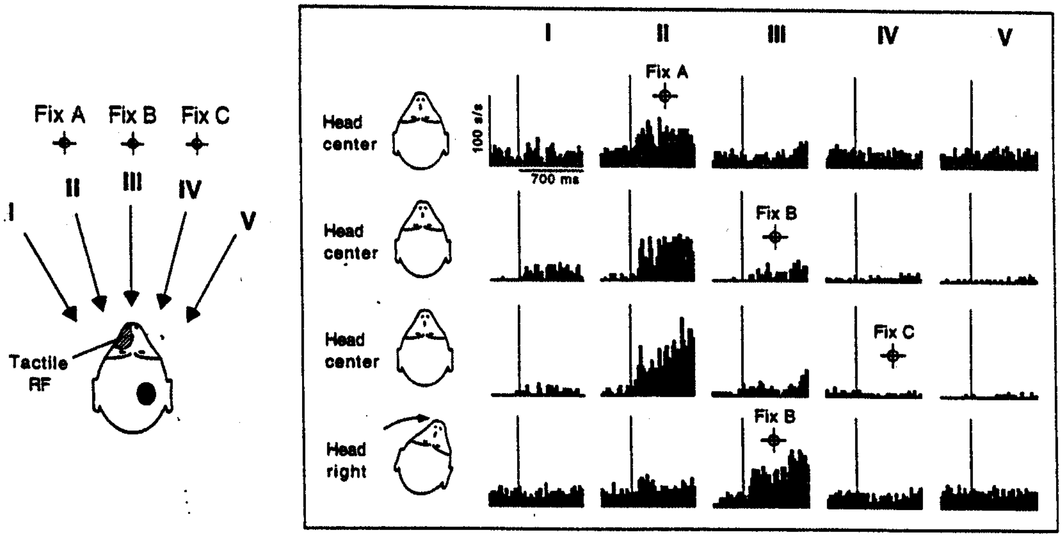

Figure 7: Left. Experimental paradigm for testing cells with receptive fields on the face. On each trial the animal fixated one of three lights 15° apart (A, B or C) and the stimulus was advanced along one of five trajectories (I-V). The head was fixed in one of three positions 15° apart. The stippling shows the tactile receptive field of the cell whose responses are illustrated on the right. Right. Histograms of neuronal activity, summed over 10 trials, as a function of eye position (A, B, C), stimulus position (I-V), and head position. When the head was straight, the neuron responded best to the stimulus II, whether the eye looked to the left (A), to the center (B), or to the right (C). However, when the head was fixed to the right, the neuron responded best to stimulus trajectory III. That is, the visual receptive field moved with the head.

OTHER BODY-PART CENTERED COORDINATES

We suggest that other brain structures concerned with sensory-motor integration also employ a similar body-part-centered strategy for the visual guidance of movement. Neurons in the frontal eye fields, parietal area LIP and the deeper layers of the superior colliculus guide saccadic eye movements in retinal coordinates and have visual, auditory and memory fields that are "attached" to the eye and move as it moves [10, 19, 47]. That is, they too use body-part-centered coordinates: in their case the body part is the eye, and the purpose is to direct the fovea toward the target.

Another interesting test of our hypothesis would involve species of animals that have unique motor hardware. For example, an elephant might use a proboscocentric coordinate system, a capuchin might use a caudocentric coordinate system, and an octopus might use a tentaculocentric coordinate system. The advantage of such body-part-centered coordinates is that sensory information about the location of the target can serve as a motor error signal guiding the movement to the target.

MULTIPLE MAPS OF SPACE AND THE PARIETAL SYNDROME

A general principle that is beginning to emerge from electrophysiological studies in the monkey is that space is encoded in different brain structures for different behavioral functions, e.g., PMv and the putamen for visuo-motor space; FEF, LIP and the colliculus for oculomotor space; and the lateral prefrontal cortex (area 46) for short-term mnemonic space [26]. In the rat, and possibly in the monkey, the hippocampus appears to be important for navigational space [40]. Each of these areas carries on, in a specialized fashion, the processing of information about space that begins in parietal cortex. This view of a multiplicity of spatial structures and coordinate systems contrasts with previous views that all of visual space is encoded by one master coordinate system, probably centered on the head or the trunk, and located in the posterior parietal cortex.

This formulation of how spatial information is organized in the brain helps explain the range and variety of visuo-spatial deficits that result from posterior parietal lesions. Such lesions not only directly disrupt the several parietal areas concerned with somatic and visual space, but also cut off the critical inputs to a widespread system of mechanisms underlying the perception and memory of space and the visual guidance of movement.

Acknowledgements

We would like to thank Xin Tian Hu, Holly Biola, Gregory Yap, Hillary Rodman, Nina Rebbman, and Allen Repp for their help. This work was suppored by NIH grant MH-19420 and NASA grant 93-330.

References

[1] G. E. Alexander, "Selective neuronal discharge in monkey putamen reflects intended direction of planned limb movements," *Experimental Brain Research*, vol. 67, pp. 623-634, 1987.

[2] G. E. Alexander, M. R. Delong, and P. L. Strick, "Parallel organization of functionally segregated circuits linking basal ganglia and cortex," *Annual Review of Neuroscience*, vol. 9, pp. 357-381, 1986.

[3] R. A. Andersen, "Inferior parietal lobule function in spatial perception and visuomotor integration," in *Handbook of Physiology*, 1987, pp. 483-518.

[4] R. A. Andersen, G. K. Essick, and R. M. Siegel, "Encoding of spatial location by posterior parietal neurons," *Science* , vol. 230, pp. 456-458, 1985.

[5] R. A. Andersen, L. H. Snyder, C. S. Li, and B. Stricanne, "Coordinate transformations in the representation of spatial information," *Current Opinion in Neurobiology*, vol. 3, pp. 171-176, 1993.

[6] R. Balint, "Seelenlähmung des 'Schauens,' optische Ataxie, raümliche Störung der Aufmerksamkeit," *Monatsschr. Psychiatr. Neurol.*, vol. 25, pp. 51-81, 1909.

[7] E. Bisiach and G. Vallar, "Hemineglect in humans," in *Handbook of Neuropsychology*, 1978, pp. 195-222.

[8] W. R. Brain, "Visual disorientation with special reference to lesions of the right cerebral hemisphere," *Brain* , vol. 263, pp. 244-272, 1941.

[9] P. R. Brotchie and R. A. Andersen, "A body centered coordinate system in posterior parietal cortex," *Society for Neuroscience Abstracts,* vol. 17, p. 1281, 1991.

[10] C. J. Bruce, "Integration of sensory and motor signals in primate frontal eye fields," in *From Signal and Sense: Local and Global Order in Perceptual Maps*, 1990, pp. 261-314.

[11] 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,* vol. 10, pp. 2039-2058, 1990.

[12] C. Cavada and P. S. Goldman-Rakic, "Posterior parietal cortex in rhesus monkey: II. Evidence for segregated corticocortical networks linking sensory and limbic areas with the frontal lobe," *Journal of Comparative Neurology,* vol. 287, pp. 422-445, 1989.

[13] C. Cavada, and P.S. Goldman-Rakic, "Topographic segregation of corticostriatal projections from posterior parietal subdivisions in the macaque monkey. *Neuroscience,* Vol. 42, pp. 683-696, 1991.

[14] C. L. Colby and J. R. Duhamel, "Heterogeneity of extrastriate visual areas and multiple parietal areas in the macaque monkey," *Neuropsychologia* , vol. 29, pp. 517-538, 1991.

[15] M. D. Crutcher and M. R. DeLong, "Single cell studies of the primate putamen. I. Functional organization," *Experimental Brain Research,* vol. 53, pp. 233-243, 1984.

[16] M. D. Crutcher and M. R. DeLong, "Single cell studies of the primate putamen. II. Relations to direction of movement and pattern of muscular activity," *Experimental Brain Research,* vol. 53, pp. 244-258, 1984.

[17] E. De Renzi, *Disorders of Space Exploration and Cognition,* New York: John Wiley & Sons, 1982.

[18] R. Desimone, and L. G. Ungerleider, "Neural mechanisms of visual processing in monkeys," in *Handbook of Neuropsychology,* Vol. 2, 1989, pp. 267-299.

[19] J. Duhamel, C. L. Colby, and M. E. Goldberg, "The updating of the representation of visual space in parietal cortex by intended eye movements," *Science,* vol. 255, pp. 90-92, 1992.

[20] D. J. Felleman and D. C. Van Essen, "Distributed hierarchical processing in primate cerebral cortex," *Cerebral Cortex,* vol. 1, pp. 1-48, 1991.

[21] L. Fogassi, V. Gallese, G. di Pellegrino, L. Fadiga, M. Gentilucci, G. Luppino, M. Matelli, A. Pedotti, and G. Rizzolatti, "Space coding by premotor cortex," *Experimental Brain Research,* vol. 89, pp. 686-690, 1992.

[22] C. Galletti, P. P. Battaglini, and P. Fattori, "Parietal neurons encoding spatial locations in craniotopic coordinates," *Experimental Brain Research,* vol. 96, pp. 221-229, 1993.

[23] M. Gentilucci, L. Fogassi, G. Luppino, M. Matelli, R. Camarda, and G. Rizzolatti, "Functional organization of inferior area 6 in the macaque monkey. I. Somatotopy and the control of proximal movements," *Experimental Brain Research,* vol. 71, pp. 475-490, 1988.

[24] A. P. Georgopoulos, "Higher order motor control," *Annual Review of Neuroscience,* vol. 14, pp. 361-377, 1991.

[25] J. Gerstmann, "Fingeragnosie: Eine umschriebene Störung der Orientierung am eigenen Körper," *Wien Klin Wochenschr*, vol. 37, pp. 1010-1012, 1924.

[26] P. S. Goldman-Rakic, S. Funahashi, and C. J. Bruce, in *The Brain*, 1990, pp. 1025-1038.

[27] M. A.Goodale, J. P. Meenan, H. Bültoff, D. A. Nicolle, K. J. Murphy, and C. I. Racicot, "Separate neural pathways for the visual analysis of object shape in perception and prehension," *Current Biology* vol. 4, pp. 604-610, 1994.

[28] M. S. A. Graziano and C. G. Gross, "A bimodal map of space: somatosensory receptive fields in the macaque putamen with corresponding visual receptive fields," *Experimental Brain Research*, vol. 97, pp. 96-109, 1993.

[29] M. S. A. Graziano and C. G. Gross, "Mapping space with neurons," *Current Directions in Psychological Science*, vol. 3, pp. 164-167, 1994.

[30] M. S. A. Graziano and C. G. Gross, "Multiple pathways for processing visual space," *Attention and Performance*, vol. 16, in press.

[31] M. S. A. Graziano and C. G. Gross, "The representation of extrapersonal space. A possible role for bimodal, visual-tactile neurons," in *The Cognitive Neurosciences*, 1994, pp. 1021-1034.

[32] M. S. A. Graziano, G. S. Yap, and C. G. Gross, "Coding of visual space by premotor neurons," *Science*, vol. 266, pp. 1054-1057, 1994.

[33] C. G. Gross, "How inferior temporal cortex became a visual area," *Cerebral Cortex*, vol. 5, pp. 455-469, 1994.

[34] C. G. Gross and M. S. A. Graziano, "Multiple representations of space in the brain," *The Neuroscientist*, vol. 1, pp. 43-50, 1995.

[35] M. S. A. Graziano and C. G. Gross, "Somatotopically organized maps of near visual space exist," *Behavioral Brain Science*, vol. 15, pp. 750, 1992.

[36] G. Holmes, "Disturbances of visual orientation," *British Journal of Ophthalmology*, vol. 2, pp. 449-516, 1918.

[37] E. R. Kandel, J. H. Schwartz, and T. M. Jessell, *Principles of Neural Science, 3rd Edition*, New York: Elsevier, 1991.

[38] S. L. Liles, "Activity of neurons in putamen during active and passive movement of wrist," *Journal of Neurohysiology*, vol. 53, pp. 217-236, 1985.

[39] M. Matelli, R. Camarda, M. Glickstein, and G. Rizzolatti, "Afferent and efferent projections of the inferior area 6 in the macaque monkey," *Journal of Comparative Neurology*, vol. 251, pp. 281-298, 1986.

[40] J. O'Keefe and L. Nadal, *The Hippocampus as a Cognitive Map*, Oxford: Oxford University Press, 1978.

[41] H. B. Parthasarathy, J. D. Schall, and A. M. Graybiel, "Distributed but convergent ordering of corticostriatal projections: Analysis of the frontal eye field and the supplementary eye field in the macaque monkey," *Journal of Neuroscience*, vol. 12, pp. 4468-4488, 1992.

[42] A. Pouget, S. A. Fischer, and T. J. Sejnowski, "Egocentric spatial representation in early vision," *Journal of Cognitive Neuroscience*, vol. 5, pp. 150-161, 1993.

[43] G. Rizzolatti, R. Camarda, L. Fogossi, M. Gentilucci, G. Luppino, and M. Matelli, "Functional organization of inferior area 6 in the macaque monkey. II. Area F5 and the control of distal movements, " *Experimental Brain Research,* vol. 71, pp. 491-507, 1988.

[44] G. Rizzolatti, C. Scandolara, M. Matelli, M. Gentilucci, "Afferent properties of periarculate neurons in macaque monkeys. II. Visual responses," *Behavioral Brain Research,* vol. 2, pp.147-163, 1981.

[45] J. D. Schall, "Neuronal activity related to visually guided saccadic eye movements in the supplementary motor area of rhesus monkeys," *Journal of Neurophysiology,* vol. 66, pp. 530-558, 1991.

[46] J. Schlag and M. Schlag-Rey, "Evidence for a supplementary eye field," *Journal of Neurophysiology,* vol. 57, pp. 179-200, 1987.

[47] D. L. Sparks, "The neural encoding of the location of targets for saccadic eye movements," in *Brain and Space,* 1991, pp. 3-19.

[48] D. L. Sparks and L. E. Mays, "Signal transformations required for the generation of saccadic eye movements," *Annual Review of Neuroscience,* vol. 13, pp. 309-336, 1990.

[49] B. E. Stein and M. A. Meredith, *The Merging of the Senses,* Cambridge: MIT Press, 1993.

[50] J. F. Stein, "Space and the parietal association areas," In: *Brain and Space,* 1991, pp. 185-222.

[51] E. J. Tehovnick and K. Lee, "The dorsomedial frontal cortex of the rhesus monkey: topographic representation of saccades evoked by electrical stimulation." *Experimental Brain Research,* vol. 96, pp. 430-442, 1993.

[52] S. P. Wise, "The primate premotor cortex: Past, present, and preparatory," *Annual Review of Neuroscience,* vol. 8, pp. 1-19, 1985.

[53] D. Zipser and R. A. Andersen, "Back propagation learning simulates response properties of a subset of posterior parietal neurons," *Nature,* vol. 331, pp. 679-684, 1988.