

Chapter 7

Visual Topography and Function

Cortical Visual Areas in the Owl Monkey

***John M. Allman, James F. Baker,
William T. Newsome and
Steven E. Petersen***

*Division of Biology, California Institute of
Technology, Pasadena, CA 91125*

1. Topographic Organization

The functional division of labor among the large number of visual areas in the cerebral cortex in primates constitutes one of the great scientific riddles in biology. The topographic organization of many of these areas was first mapped in the owl monkey (2-7, 39). The cortical visual areas of the owl monkey are illustrated in an unfolded schema in Fig. 7.1 and as they are located in the brain in Fig.

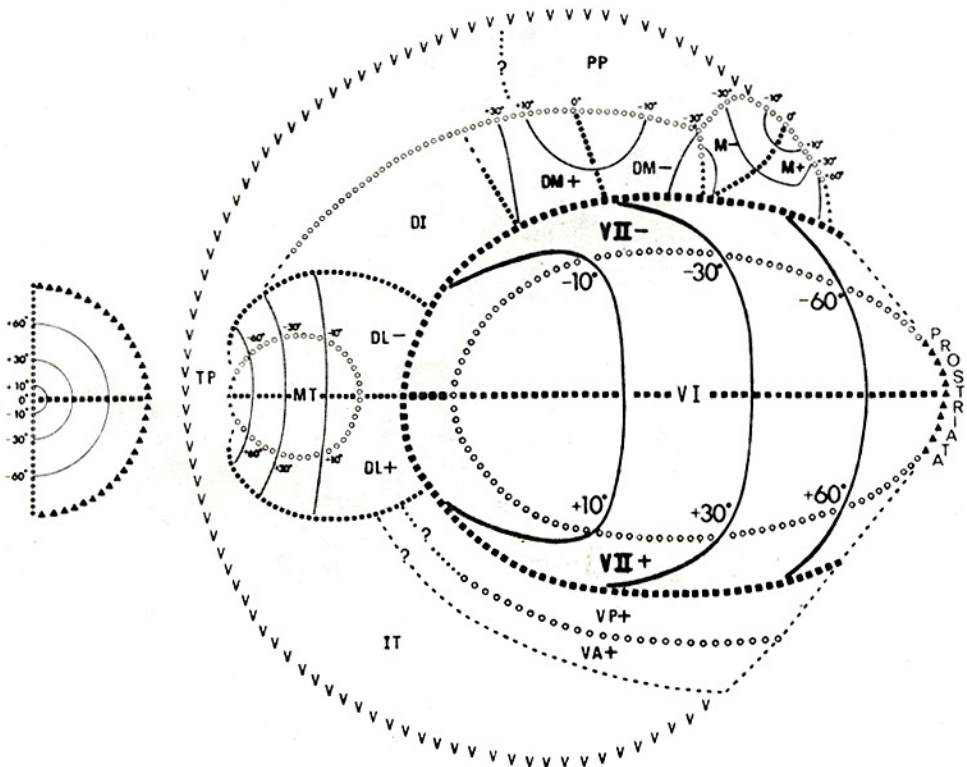


FIG. 7.1. A schematic unfolding of the visual cortex of the left hemisphere of the owl monkey. The visual cortex corresponds to approximately the posterior third of the entire neocortex. The unfolded visual cortex is approximately a hemispherical surface, which is viewed from above in this diagram. The perimeter chart on the left shows the contralateral (right) half of the visual field. The symbols in this chart are superimposed on the surface of the visual cortex. Pluses indicate upper quadrant representations; minuses, lower quadrants; dashed lines, borders of areas that correspond to the representation of the relatively peripheral parts of the visual field, but not to the extreme periphery. The row of Vs indicates the approximate anterior border of visually responsive cortex. The dotted lines broken by question marks indicate uncertain borders. DI, Dorsointermediate Visual Area; DL, Dorsolateral Crescent Visual Area; DM, Dorsomedial Visual Area; IT, inferotemporal Cortex; M, Medial Visual Area; MT, Middle Temporal Visual Area. PP, Posterior Parietal Cortex; VA, Ventral Anterior Visual Area; VP, Ventral Posterior Visual Area.

7.2. Areas V I and V II share a common border, along which the vertical meridian or midline of the visual field is represented in each area. In each hemisphere V I contains a topological, first-order transformation, of the contralateral half of the visual field, in which the more central portions are greatly expanded (3). In V II, the repre-

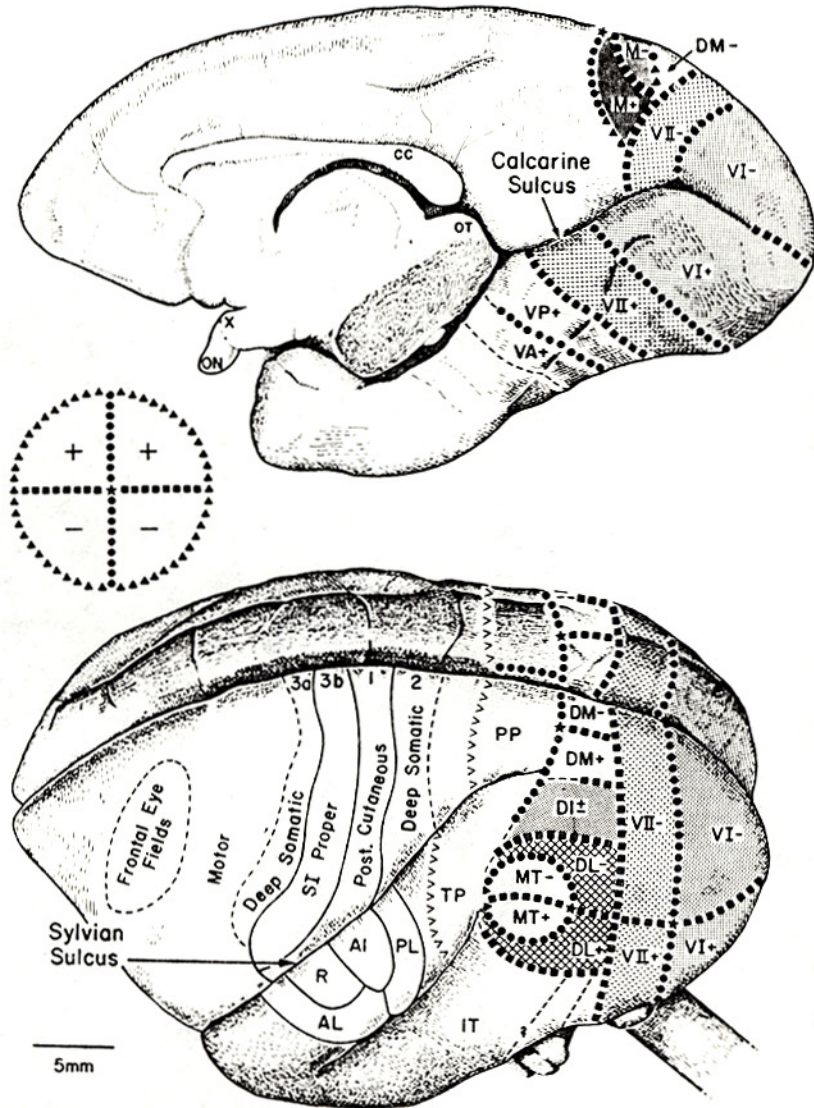


FIG. 7.2. The representation of the sensory domains in the cerebral cortex of the owl monkey. Above is a ventromedial view of the right hemisphere; below is a dorsolateral view. First Auditory Area: AL. Anterolateral Auditory Area; CC, Corpus Callosum; ON, Optic Nerve, OT, Optic Tectum; PL, Posterolateral Auditory Areas; R, Rostral Auditory Area. The cortical visual areas were mapped by Allman and Kaas (2-7) and Newsome and Allman (39); the somatosensory areas were mapped by Merzenich et al. (36); the auditory areas were mapped by Imig et al. (27). Other conventions and abbreviations are as in Fig. 7.1. Reproduced from reference 10 by permission of the American Physiological Society

sensation of the horizontal meridian is split except near the center of gaze (4). Since adjacent parts of the contralateral hemifield are not necessarily mapped onto adjacent parts of V II, the representation of the hemifield is not topological and has been termed a second order transformation (4). The Middle Temporal Area (MT) and the Dorsolateral Area (DL) form a miniature mirror-image of V I and V II (5). DL, together with the Medial (M), the Dorsointermediate (DI), the Dorsomedial (DM) and the Ventroposterior (VP) Areas, constitute a third tier of cortical visual areas that adjoin the anterior border of V II (5, 6, 7, 39) (V I is the first tier; V II the second). Two visuotopically organized fourth tier areas are known: MT and the recently discovered Ventral Anterior Area (VA) (2, 39). Each of these shares a border corresponding to a vertical meridian representation with a third tier area. The possibility exists that additional fourth tier areas will be discovered in the visually responsive posterior parietal (PP) or temporal parietal (TP) cortex that will be the mates to adjacent third tier areas. Finally, there is a large region of visually responsive cortex in the inferior temporal gyrus (IT) anterior to VA and DL. Only the posterior third of this region has been explored in the owl monkey and this zone contains neurons with receptive fields predominantly in the central visual field and with no apparent visuotopic organization (1). These results are similar to those obtained by Desimone and Gross (15) over a much broader region of the inferior temporal gyrus in macaque monkeys.

Several principles emerge from the topographic organization of the cortical visual areas.

1. A surprisingly large number of visuotopically organized areas exists—at least nine.

2. Since each of these exists as an anatomical entity, it is probable that each is a functional entity as well.

3. The areas group themselves into a number of larger (and not mutually exclusive) sets. These include the dyads that have adjoining vertical meridian representations: V I–V II, MT–DL and VP–VA. Other groupings include: the first-order transformations (VI and MT); the second order transformations (V II, DL, DM, M); the third tier (M, DM, DI, DL and VP); and the fourth tier (MT and VA). The areas in these sets may have important functional or developmental attributes in common.

4. The areas are juxtaposed so that their common borders correspond nearly always to portions of either the horizontal or the vertical meridian and the adjacent points on opposite sides of each border nearly always have similarly positioned receptive fields. Thus, there is very little disruption of visuotopic order at the interfaces between areas.

5. The relative representation of different portions of the visual field varies greatly among areas. Area V I has been widely assumed to contain a representation proportional to retinal ganglion cell density; however, recent analysis has shown that the representation of the central visual field in V I is very much greater relative to the periphery than could be accounted for on the basis of a proportional relationship (38). Each area has its own unique way of mapping the visual field and this mapping is likely to reflect the functions performed by that area (see Fig. 7.3). The representation of the central 10° of the visual field occupies 31% of the surface area of V I as compared to 75% of DL, which contains proportionally the largest expansion of the central visual field of all the areas (5). Only 4% is devoted to the central 10° of M, where the more peripheral parts of the visual field are relatively much better represented than in any other area (7).

6. Finally, there exists an important principle of topographic organization that cannot be deduced from these figures. Cortical visual areas differ in their visuotopic orderliness. Although we have not developed a direct quantitative measure of topographic orderliness, our experiences suggest that V I is the most orderly, followed

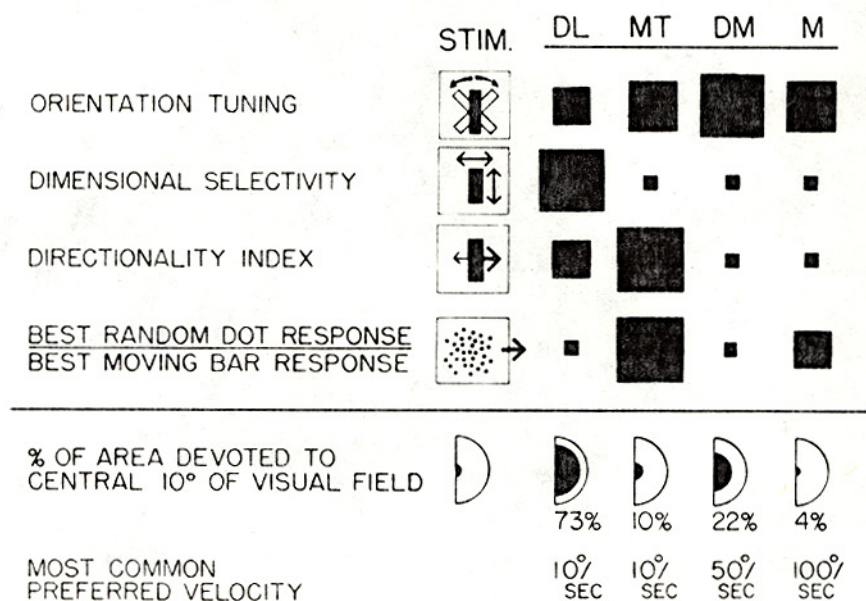


FIG. 7.3. Functional specificity in visual areas DL, MT, DM and M in the owl monkey. The strength of the functional attribute is indicated by the size of the black squares.

by V II, then by VP and VA, then by MT, DM and M. DL appears to be the least orderly of the mapped areas. One measure of the topographic order in these areas is the distribution of callosal terminals following section of the corpus callosum, which contains fibers that unify the two halves of the visual field along the vertical meridian (midline). The callosal terminals are largely restricted to a narrow zone on each side of the common border between V I and V II, along which the vertical meridian (midline) is represented (39). Along the border between VP and VA, callosal terminals are confined to a band that is nearly as discrete as that found at the V I-V II border and also corresponds to the representation of the vertical meridian (39). Callosal terminals form more diffuse zones of degeneration near the vertical meridian representations in MT, DM and M (39). Callosal terminals are distributed throughout most of DL, which contains large receptive fields that often overlap the vertical meridian (39, 42). Posterior Parietal (PP) and Temporal Parietal (TP) cortex may contain visuotopically organized areas, although it is difficult to discern a pattern, since receptive fields tend to be large and callosal connections diffuse in these regions. Finally, receptive fields in inferotemporal cortex (IT) tend to be located in the central visual field but do not appear to have a visuotopic organization (1). What organizing principle does prevail in this large expanse of visual cortex in the inferior temporal gyrus remains a tantalizing question. The topographic organization of IT may be related to its projections to perirhinal cortex and the amygdala and the related functions of visual memory and visual perception of emotionally significant stimuli (52).

2. Functional Correlates

Our guiding hypothesis has been that each cortical representation of the visual field performs its own set of neural functions, some of which are distinctive to that particular area. Our approach to determining the functions of cortical visual areas has been to analyze quantitatively the response properties of single neurons in each area in order to discover how information is processed in that area.

The procedures employed for recording from single neurons in the cortical visual areas of owl monkeys are described in detail elsewhere (10, 42). Briefly, in order to make more efficient use of our owl monkeys, we have developed a chronic technique for recording repeatedly from the visual cortex in monkeys that have been tranquilized with light doses of triflupromazine and ketamine and their

locally anesthetized eyes held stable by rings machined to fit the contour of the eyes. The visuotopic organization of the region of exposed cortex beneath the chronically implanted recording chamber was mapped in order to identify the location and boundaries of visual areas, so that recorded single neurons could be assigned to a particular area. Small electrolytic lesions were made at the end of selected microelectrode penetrations, identified in histological sections and compared with the known cyto- and myeloarchitecture of the cortical visual area (2-6). Visual stimuli were light and dark bars, spots and textures focused on a tangent screen by a rear projection optic stimulator. After receptive field mapping and initial qualitative examination, the response properties were studied quantitatively using the optic stimulator in conjunction with a Nova 2 computer. For each stimulus parameter (orientation, direction of movement, etc.), the stimuli were presented in pseudorandom order so as to average out any periodic waxing and waning in a cell's responsiveness and to avoid possible habituating effects that may occur when the same stimulus is presented repeatedly (24). The computer recorded the neuron's spontaneous firing during an interval preceding the stimulus presentation and calculated its response relative to the level of spontaneous activity. From these data, the computer calculated a series of indices that enabled us to compare objectively the response profiles of the populations of neurons obtained from MT, DL, DM and M for orientation tuning and selectivity for direction of movement and stimulus dimensions. The following is a summary of these results (10, 42).

1. Neurons in DL, MT, DM and M are orientation selective. As in VI (36), neurons in these four extrastriate areas tend to be orientation selective, when tested with stationary flashed or moving bars; however, there are statistically significant differences among the areas in sharpness of tuning for orientation with DM neurons being the most selective, MT and M neurons intermediate and DL neurons least tuned (10).

2. In DL, about 70% of the neurons are selective for the spatial dimensions of visual stimuli within excitatory receptive fields that are generally much larger than the preferred stimulus dimensions. The dimensional selectivity of DL cells is independent of the sign of contrast in the receptive field (equal to light-on-dark and dark-on-light stimuli), the amount of contrast (similar response over a 1.5 log unit change in intensity) and the position of the stimulus within the receptive field. DL neurons have a wide range of preferred sizes, from 1 to 30° in length and from 0.25 to 7° in width, and these preferences appeared to be independent of each other, when both dimensions were tested on the same cell (42). The dimensional selectivity of DL neurons suggests that DL contributes

to form perception. This hypothesis is consistent with the observation that DL has the most expanded representation of the central visual field (5), where the most acute recognition of form takes place, and the recent discovery that DL is the main source of input to the inferotemporal cortex (58). Inferotemporal cortex has been strongly implicated in the analysis of complex visual stimuli and the learning of visual form discriminations (20, 21). DL is thus an intermediate stage in a major ascending system from layers II and III in V I, to V II, to DL, to IT, and thence to the amygdala and perirhinal cortex (52, 57).

3. Neurons in MT discriminate strongly between stimuli moving in the preferred direction and stimuli moving in the direction 180° opposite. DL neurons generally make this discrimination less well; DM and M neurons generally discriminate this difference in direction of movement very poorly. Most MT neurons resemble the classic directionally selective cells recorded by Barlow et al. (11) in the rabbit retina and observed by many investigators in other species and at other levels in the visual system (23, 50, 56, 60).

4. Neurons in MT respond well to moving texture patterns (arrays of random dots); M neurons respond moderately well; DL and DM neurons respond poorly. All MT cells responded to the moving random dot array and the majority responded better to the array than to the optimally oriented bar moving in its optimal direction and at its optimal velocity. Some neurons in the deeper layers of MT respond well to random dot arrays, but are unresponsive to bar stimuli. All cells tested in M also were responsive to the moving array and one third responded better to the array than to the best bar stimulus. About half the neurons in DL and DM were unresponsive to the moving array and most of the remainder responded poorly to this stimulus. These differences in responsiveness to random dot arrays parallel the discovery, by Hammond and McKay (22) in V I of the cat, that complex cells are responsive to random arrays whereas simple cells are not. It is not known whether there exists a similar dichotomy in responsiveness to textured arrays among neurons in V I in the owl monkey. The striate neurons projecting to MT are the giant cells of Meynert (32, 47, 57), located in the lower parts of layer V, and the neurons located in or near the stria of Gennari. Both these populations of striate neurons are capable of sampling neural activity over relatively large regions. The Meynert cells are by far the largest in striate cortex and their basal dendrites extend for hundreds of micra (13); the layer IVb neurons are located in a dense fiber plexus that was once thought to be the terminations of the geniculate fibers, but has now been shown to be made up to many elements (32). Thus, the striate neurons projecting to

MT could sample over the relatively large regions necessary for the detection of texture arrays. In addition, Montero (37) has demonstrated that there is a relatively large overlap in the projection to MT of different sites in V I by using double-label emulsion autoradiography. MT projects to M (57). MT and M project to the visual pontine nuclei (17, 18), which contain a large proportion of neurons that are especially responsive to moving random dot arrays (9). The pontine nuclei, in turn, project to the cerebellum, where the relayed information presumably contributes to the accomplishment of visuomotor coordination.

5. Neurons in DL, MT, DM and M differ in their distributions of preferred velocities of stimulus movement. The neurons were tested with stimulus velocities ranging from 5°/s to 500°/s. The most common preferred velocity was 10°/s in DL and MT, 50°/s in DM and 100°/s in M. The high preferred stimulus velocities in M may be related to the proportionally large representation of the peripheral visual field in this area (7).

3. Homologous Cortical Visual Areas in Other Species

Beyond V I and V II, the clearest homology is that of MT and similar visual areas in other primate species. The evidence for homology is based on similar location, myeloarchitecture, topography, distinctive anatomical connectivity and visual response properties (1, 2, 8, 10, 12, 21, 46, 49, 53, 54, 57). Owl monkey MT is striate-receptive region of dense myelination coextensive with an orderly map of the visual hemifield (2). A corresponding striate-receptive region of dense myelination coextensive with a similar map of the visual field has been reported in galago (8, 51), marmoset (48, 49) and macaque (16, 35, 55, 56). A major source of input to MT in the owl monkey is from V I cells in or near the stria of Gennari and from the giant cells of Meynert located in the lower part of layer V (57). A similar projection occurs in marmoset (47) and macaque (32) from striate cortex cells in the stria of Gennari and the giant Meynert cells. MT is the only known extrastriate cortical target of the Meynert cells (33). Directional selectivity is the principal characteristic of owl monkey MT cell responses, and this has been shown to be true for the ecorresponding region of the macaque (60). The presence of these extensive and detailed similarities in three superfamilies of primates, including primates from both infraorders, indicates that MT probably existed in the early primates ancestral to all living prima-

tes. Zeki (61) recently has suggested that MT in the owl monkey is not homologous with the striate-receptive, densely myelinated, directionally selective zone in the posterior bank of the superior temporal sulcus in macaque monkeys; his suggestion is considered in detail in ref. 10.

In our present state of knowledge, it is more difficult to establish clear-cut homologies for the other visual areas found beyond V II in the owl monkey. However, evidence for the homology of several areas is emerging. The principal input to infero-temporal visual cortex in the owl monkey is DL (58). In macaques, a region adjacent to MT is a main input to inferotemporal cortex (14). This region, like DL in the owl monkey, emphasizes the representation of the central visual field (15). MT in both owl monkeys and macaques does not appear to project to inferotemporal cortex. The position of DL between MT and V II in owl monkey is topographically similar to V IV (V 4) in macaques. Neurons in V IV (V 4) have been reported to be specialized for the analysis of color but the percentage of neurons showing color selectivity in V IV (V 4) has ranged from 100% in the original report (59) to less than one third in more recent studies (45, 55). Another recent report suggests that color processing in V IV (V 4) is substantially similar to the color selectivity found in foveal V I and V II (30).

Another potential homology is that of the Ventral Posterior (VP) areas of the owl monkey and the macaque (39, 40). These areas are similar in that they both are long narrow strips that lie immediately anterior to V II on the ventral surface, with this common border corresponding to a representation of the horizontal meridian. In both monkeys, the anterior border of VP corresponds to a discrete band of degeneration following section of the corpus callosum. In both monkeys, the visual field representation in VP appears to be limited to the upper quadrant with the more central portions represented laterally and the more peripheral portions medially. The establishment of potential homologies for DM and M awaits further investigation.

Outside of primates, it is much more difficult to establish homologies. The last common ancestor of the different mammalian orders lived no more recently than the late Cretaceous period more than 60 million years ago (43). This ancestral mammal had only a very limited development of its neocortex (29). In addition, the adaptive radiation of mammals into different ecological niches with widely divergent behavioral specializations serves to make very difficult the discovery of diagnostic similarities among potentially homologous cortical areas in different mammalian orders. These nonprimate candidates for homology are discussed in reference 10.

4. Significance of Multiple Cortical Areas

Why does the cerebral cortex contain a series of separate representations rather than a single map? In attempting to develop computer analogues of visual perception, Marr elaborated the principle of modular design. Marr (34) stated that any large computation should be broken into a collection of smaller modules as independent as possible from one another. Otherwise, "the process as a whole becomes extremely difficult to debug or improve, whether by a human designer or in the course of natural evolution, because a small change to improve one part has to be accompanied by many simultaneous changes elsewhere." This modular principle has many counterparts in other biological systems. The paleontologist Gregory (19) noted that a common mechanism of evolution is the replication of body parts due to genetic mutation in a single generation, which is followed in subsequent generations by the gradual divergence of structure and functions of the duplicated parts. An analogous idea has been advanced by a number of geneticists. They have theorized that replicated genes escape the pressures of natural selection operating on the original gene and thereby can accumulate mutations, which enable the new gene, through changes in its DNA sequence, to encode for a novel protein capable of assuming new functions (31, 41). Many clearcut examples of gene replication have been discovered (28), and DNA sequence homologies in replicated genes recently have been established (44). Using this analogy, Allman and Kaas (2, 5) have proposed that the replication of cortical sensory representations has provided the structures upon which new information processing capabilities have developed in the course of evolution. Specifically, it has been argued that existing cortical areas, like genes, can undergo only limited changes and still perform the functions necessary for the animal's survival, but if a mutation occurs that results in the replication of a cortical area, then in subsequent generations the new area can eventually assume new functions through the mechanisms of natural selection, while the original area continues to perform its function.

Acknowledgments

We thank Fran Miezin for developing many of the computer programs used in this study and Leslie Wolcott for drawing the figures. This research was supported by NIH grants NS-00178, NS-12131

and GM-07737, NSF grant BNS-77-15605 and the Pew Memorial Trust.

References

1. ALLMAN, J. M. Evolution of the visual system in the early primates. In: *Progr. Psychobiol. Physiol. Psych.*, vol 7, edited by J. M. Sprague and A. N. Eptsein. New York: Academic Press, 1977, pp. 1-53.
2. ALLMAN, J. M., AND KAAS, J. H. A representation of the visual field in the caudal third of the middle temporal gyrus of the owl monkey (*Aotus trivirgatus*). *Brain Res.*, 31: 84-105, 1971.
3. ALLMAN, J. M., AND KAAS, J. H. Representation of the visual field in striate and adjoining cortex of the owl monkey (*Aotus trivirgatus*). *Brain Res.*, 35: 89-106, 1971.
4. ALLMAN, J. M., AND KAAS, J. H. The organization of the second visual area (V II) in the owl monkey: A second order transformation of the visual hemifield. *Brain Res.*, 76: 247-265, 1974.
5. ALLMAN, J. M., AND KAAS, J. H. A crescent-shaped cortical visual area surrounding the middle temporal area (MT) in the owl monkey (*Aotus trivirgatus*). *Brain Res.*, 199-213, 1974.
6. ALLMAN, J. M., AND KAAS, J. H. The dorsomedial cortical visual area: A third tier area in the occipital lobe of the owl monkey (*Aotus trivirgatus*). *Brain Res.*, 100: 473-487, 1975.
7. ALLMAN, J. M., AND KAAS, J. H. Representation of the visual field on the medial wall of occipital-parietal cortex in the owl monkey. *Science*, 191: 572-575, 1976.
8. ALLMAN, J. M., KAAS, J. H., AND LANE, R. H. The middle temporal visual area (MT) in the bushbaby, *Galago senegalensis*. *Brain Res.*, 57: 197-202, 1973.
9. BAKER, J. F., GIBSON, A., GLICKSTEIN, G., AND STEIN, J. Visual cells in the pontine nuclei of the cat. *J. Physiol., London*, 255: 415-433, 1976.
10. BAKER, J. F., PETERSEN, S. E., NEWSOME, W. T., AND ALLMAN, J. M. Visual response properties of neurons in four extrastriate visual areas of the owl monkey (*Aotus trivirgatus*): A quantitative comparison of the medial (M), dorsomedial (DM), dorsolateral (DL), and middle temporal (MT) areas. *J. Neurophysiol.*, 45: 387-406, 1981.
11. BARLOW, H. B., HILL, R. M., AND LEVICK, W. R. Retinal ganglion cells responding selectively to direction and speed of image motion in the rabbit. *J. Physiol., London*, 173: 377-407, 1964.
12. CAMPBELL, C. B. G., AND HODOS, W. The concept of homology and the evolution of the nervous system. *Brain, Behav. Evol.*, 3: 353-367, 1970.
13. CHAN-PALAY, V., PALAY, S. L., AND BILLINGS-GAGLIARDI, S. M. Meynert cells in the primate visual cortex. *J. Neurocytol.*, 3: 631-658, 1974.

14. DESIMONE, R., FLEMING, J., AND GROSS, C. G. Prestriate afferents to inferior temporal cortex: an HRP study. *Brain Res.*, in press, 1981.
15. DESIMONE, R. AND GROSS, C. G. Visual areas in the temporal cortex of the macaque. *Brain Res.*, 178: 363-380, 1979.
16. GATTASS, R., AND GROSS, C. G. A visuotopically organized area in the posterior superior temporal sulcus of the macaque. *ARVO Annual Meeting Abstr.*, 1979, p. 184.
17. GLICKSTEIN, M., COHEN, J., DIXON, B., GIBSON, A., HOLLINS, M., LA BOSSIERE, E., AND ROBINSON, F. Corticopontine visual projection in the macaque monkey. *J. Comp. Neurol.*, 190: 209-230, 1980.
18. GRAHAM, J., LIN, C.-S., AND KAAS, J. H. Subcortical projections of six visual cortical areas in the owl monkey, *Aotus trivirgatus*. *J. Comp. Neurol.*, 187: 557-580, 1979.
19. GREGORY, W. K. Reduplication in evolution. *Quart. Rev. Biol.*, 10, 272-290, 1935.
20. GROSS, C. G. Visual functions of inferotemporal cortex. In: *Handbook of Sensory Physiology, VII/3 B* edited by R. Jung. Berlin: Springer, 1973, p. 451-482.
21. GROSS, C. G., BRUCE, C. J., DESIMONE, R., FLEMING, J., AND GATTASS, R. Three visual areas of the temporal lobe. *This volume*, chapter 8.
22. HAMMOND, P., AND MACKAY, D. M. Differential responsiveness of simple and complex cells in cat striate cortex to visual texture. *Exptl. Brain Res.*, 30: 106-154, 1977.
23. HUBEL, D. H., AND WIESEL, T. N. Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *J. Physiol., London*, 60: 106-154, 1962.
24. HUBEL, D. H., AND WIESEL, T. N. Receptive fields and functional architecture in two non-striate visual areas (18 and 19) of the cat. *J. Neurophysiol.*, 28: 229-289, 1965.
25. HUBEL, D. H., AND WIESEL, T. N. Visual area of the lateral suprasylvian gyrus (Clare-Bishop area) of the cat. *J. Physiol., London*, 202: 251-260, 1969.
26. HUBEL, D. H., AND WIESEL, T. N. Functional architecture of macaque monkey visual cortex. *Proc. Roy. Soc., London, B*, 198: 1-59, 1977.
27. IMIG, T. J., RUGGERO, M. A., KITZES, L. M., JAVEL, E., AND BRUGGE, J. F. Organization of auditory cortex in the owl monkey (*Aotus trivirgatus*). *J. Comp. Neurol.*, 171: 111-128, 1977.
28. INGRAM, V. M. *The Hemoglobins in Genetics and Evolution*. New York: Columbia Univ. Press, 1963.
29. JERISON, H. *Evolution of the Brain and Intelligence*. New York: Academic Press, 1973.
30. KRUGER, J., AND GOURAS, P. Spectral selectivity of cells and its dependence on slit length in monkey visual cortex. *J. Neurophysiol.*, 43: 1055-1069, 1980.
31. LEWIS, E. B. Pseudoallelism and gene evolution. *Cold Spring Harbor Symp. Quant. Biol.*, 16: 159-174, 1951.

32. LUND, J. S., LUND, R. D., HENDRICKSON, A. E., BUNT, A. H., AND FUCHS, A. F. The origin of efferent pathways from the primary visual cortex, area 17, of the macaque monkey as shown by retrograde transport of horseradish peroxidase. *J. Comp. Neurol.*, 164: 287-304, 1976.
33. LUND, J. S., HENRY, T. H., MACQUEEN, C. L., AND HARVEY, A. R. Anatomical organization of the primary visual cortex (area 17) of the cat. A comparison with area 17 of the macaque monkey. *J. Comp. Neurol.*, 184: 599-618, 1979.
34. MARR, D. Early processing of visual information. *Phil. Trans. Roy. Soc., London, Series B*, 275: 484-519, 1976.
35. MAUNSELL, J. H. R., BIXBY, J. L., AND VAN ESSEN, D. C. The middle temporal (MT) area in the macaque: Architecture, functional properties and topographic organization. *Soc. Neurosci. Abstr.*, 5: 796, 1979.
36. MERZENICH, M. M., KAAS, J. H., SUR, M., AND LIN, C.-S. Double representation of the body surface within cytoarchitectonic areas 3b and 1 in SI in the owl monkey (*Aotus trivirgatus*). *J. Comp. Neurol.*, 181: 41-74, 1978.
37. MONTERO, V. M. Patterns of connections from the striate cortex to cortical visual areas in superior temporal sulcus of macaque and middle temporal gyrus of owl monkey. *J. Comp. Neurol.*, 189: 45-55, 1980.
38. MYERSON, J., MANIS, P. B., MIEZIN, F. M., AND ALLMAN, J. M. Magnification in striate cortex and retinal ganglion cell layer of owl monkeys: A quantitative comparison. *Science*, 198: 855-857, 1977.
39. NEWSOME, W. T., AND ALLMAN, J. M. The interhemispheric connections of visual cortex in the owl monkey, *Aotus trivirgatus*, and the bushbaby, *Galago senegalensis*. *J. Comp. Neurol.*, 194: 209-233, 1980.
40. NEWSOME, T. W., MAUNSELL, J. H. R., AND VAN ESSEN, D. C. Areal boundaries and topographic organization of the ventral posterior area (VP) of the macaque monkey. *Soc. Neurosci. Abstr.*, 6: 579, 1980.
41. OHNO, S. *Evolution by Gene Duplication*. New York: Spring, 1970, p. 1-60.
42. PETERSEN, S. E., BAKER, J. F., AND ALLMAN, J. M. Dimensional selectivity of neurons in the dorsolateral visual area of the owl monkey. *Brain Res.*, 197: 507-511, 1980.
43. ROMER, A. S. *Vertebrate Paleontology*. Chicago: Univ. of Chicago Press, 1966, pp. 1-460.
44. ROYAL, A., GARAPIN, A., CAMIL, B., PERRIN, F., MANDEL, J. L., LEMEUR, J., BREGELEGRE, F., LEPENNEC, J. P., CHAMBON, P., AND KOURILSKY, P. The ovalbumin gene region: Common features in the organization of three genes expressed in chicken oviduct under hormonal control. *Nature*, 279: 125-132, 1979.
45. SCHEIN, S. J., MARRACCO, R. T., AND DE MONASTERIO, F. M. Spectral properties of cells in the prestriate cortex of monkey. *Soc. Neurosci. Abstr.*, 6: 580, 1980.

46. SIMPSON, G. G. *Principles of Animal Taxonomy*. New York: Columbia Univ. Press, 1961.
47. SPATZ, W. B. An efferent connection of the solitary cells of Meynert. A study with horseradish peroxidase in the marmoset, *Callithrix*. *Brain Res.*, 92: 450-455, 1975.
48. SPATZ, W. B. Topographically organized reciprocal connections between areas 17 and MT (visual area of the superior temporal sulcus) in the marmoset (*Callithrix jacchus*). *Exptl. Brain Res.*, 27: 559-572, 1977.
49. SPATZ, W. B., AND TIGGES, J. Experimental-anatomical studies on the Middle Temporal Visual Area (MT) in primates. I. Efferent cortico-cortical connections in the marmoset (*Callithrix jacchus*). *J. Comp. Neurol.*, 146: 451-563, 1972.
50. SPEAR, P. D., AND BAUMANN, T. P. Receptive-field characteristics of single neurons in lateral suprasylvian visual area of the cat. *J. Neurophysiol.*, 38: 1403-1420, 1975.
51. TIGGES, J., TIGGES, M., AND KALAHA, C. S. Efferent connections of area 17 in *Galago*. *Amer. J. Phys. Anthropol.*, 38: 393-398, 1973.
52. TURNER, B. H., MISHKIN, M., AND KNAPP, M. Organization of amygdalopetal projections from modality-specific cortical association areas in the monkey. *J. Comp. Neurol.*, 193: 147-184, 1980.
53. UNGERLEIDER, L. G., AND MISHKIN, M. The striate projection zone in the superior temporal sulcus of *Macaca mulatta*: Location and topographic organization. *J. Comp. Neurol.*, 188: 347-366, 1979.
54. VAN ESSEN, D. C. Visual cortical areas. In: *Ann. Rev. Neurosci.*, Vol. 2, edited by W. M. Cowan. Palo Alto: Annual Reviews, Inc., 1979, p.
55. VAN ESSEN, D. C., AND ZEKI, S. M. The topographic organization of rhesus monkey prestriate cortex. *J. Physiol., London*, 277: 193-226, 1978.
56. WELLER, R. E., KAAS, J. H. Connections of striate cortex with the posterior bank of the superior temporal sulcus in macaque monkeys. *Soc. Neurosci. Abstr.*, 4: 650, 1978.
57. WELLER, R. E., AND KAAS, J. H. Cortical and subcortical connections of visual cortex in primates. *This volume*, chapter 13.
58. WELLER, R. E., AND KAAS, J. H. Connections of the dorsolateral visual area (DL) of extrastriate visual cortex of the owl monkey (*Aotus trivirgatus*). *Soc. Neurosci. Abstr.*, 6: 579, 1980.
59. ZEKI, S. M. Colour coding in the superior temporal sulcus of rhesus monkey visual cortex. *Brain Res.*, 422-427, 1973.
60. ZEKI, S. M. Functional organization of visual area in the posterior bank of the superior temporal sulcus of the rhesus monkey. *J. Physiol., London*, 236: 549-573, 1974.
61. ZEKI, S. M. The response properties of cells in the middle temporal area (area MT) of owl monkey visual cortex. *Proc Roy. Soc. London, B*, 207: 239-248, 1980.