Visual cortex: cartography, connectivity, and concurrent processing

James J. Knierim and David C. Van Essen

California Institute of Technology, Pasadena, California, USA

The mammalian visual cortex contains a complex mosaic of areas that are richly connected with one another. Recent progress has advanced our understanding of both macroscopic and microscopic aspects of cortical organization, and of information flow within and between functionally specialized processing streams.

Current Opinion in Neurobiology 1992, **2**:150–155

Introduction

The workings of the visual cortex are a matter of fascination not only for our understanding of visual perception, but also for their relevance to other cortical functions, including cognitive processing. Several interrelated themes have figured prominently in recent studies of the organization and function of visual cortex. At a gross organizational level, visual cortex contains an impressively large number of distinct areas (dozens in some species) that are organized into a distributed hierarchy containing many levels of processing. Within this hierarchy there are intertwined processing streams related to different cell classes originating in the retina, and to different targets in the temporal and parietal lobes. At a finer level, an important theme has been the analysis of network architecture underlying specific receptive field properties. In reviewing progress on these fronts during the past year we will emphasize work on the macaque monkey, because it is the most intensively studied laboratory animal. The results from the macaque also provide a solid foundation on which to discuss the substantial progress that has recently been made in human visual cortex research and that of several other species.

Mapping the visual cortex

More than half of the cerebral cortex in the macaque monkey is largely or exclusively involved in visual processing. This overall domain of visual cortex contains an estimated 32 distinct areas that have been identified on the basis of their connectivity, architecture, topographic organization, and/or function [1••]. The size and location of different areas are most readily visualized on an unfolded two-dimensional map of the cerebral cortex (Fig.1). Many of these areas have sharply defined borders that have been identified with a high degree of confidence, even though not all laboratories use the same terminology. For many other regions, however, significant uncertainty remains about the basic partitioning plan. For example, the scheme in Fig.1 subdivides inferotemporal (IT) cortex into three pairs of areas respectively occupying posterior (PIT), central (CIT), and anterior (AIT) regions of the temporal lobe [2•]. An alternative scheme for this region is based on the TEO/TE distinction proposed by classical anatomists and recently reinvestigated in an extensive electrophysiological mapping study of TEO and surrounding cortex [3•]. Area TEO includes most or all of the posterior inferotemporal areas (PITd and PITv) as well as area VOT of Fig.1, whereas TE includes most or all of the central and anterior inferotemporal areas. These alternative partitioning schemes do not reflect gross conflicts in the underlying experimental data. The various approaches to partitioning the cortex (architectonics, topography, etc.) are often ambiguous or inadequate when applied in isolation, and even when multiple approaches are applied in conjunction the currently available data sometimes allow for more than one interpretation. Hence, Fig.1, as well as other partitioning schemes, should be regarded as a progress report subject to ongoing refinement.

The application of sensitive pathway tracing techniques has revealed a remarkably rich pattern of connectivity in the visual cortex, totalling 305 reported pathways among the 32 identified areas in the macaque [1••]. These areas can be arranged in an orderly hierarchy containing ten levels of processing, based on the laminar distribution of connections between areas. Nearly all pathways that have been appropriately examined occur in reciprocal pairs. An intriguing exception to this pattern has been reported among several areas of the temporal lobe [4]. Specifically, areas TF, TH, and 35 all project to TE, but TE apparently does not send reciprocal projections back to any of these areas. Similarly, each of these areas, plus areas TG and 36, have one-way (non-reciprocated) projections to TEO. Thus, top-down influences arising from high-level areas in the cortical hierarchy may have direct access to inferotemporal areas where visual memories are thought to be stored.

Abbreviations

CRF—classic receptive field; **IT**—inferotemporal cortex; **LGN**—lateral geniculate nucleus; **M**—magnocellular; **MRI**—magnetic resonance imaging; **P**—parvocellular; **PET**—positron emission tomography.

 ISSN 0959-4388

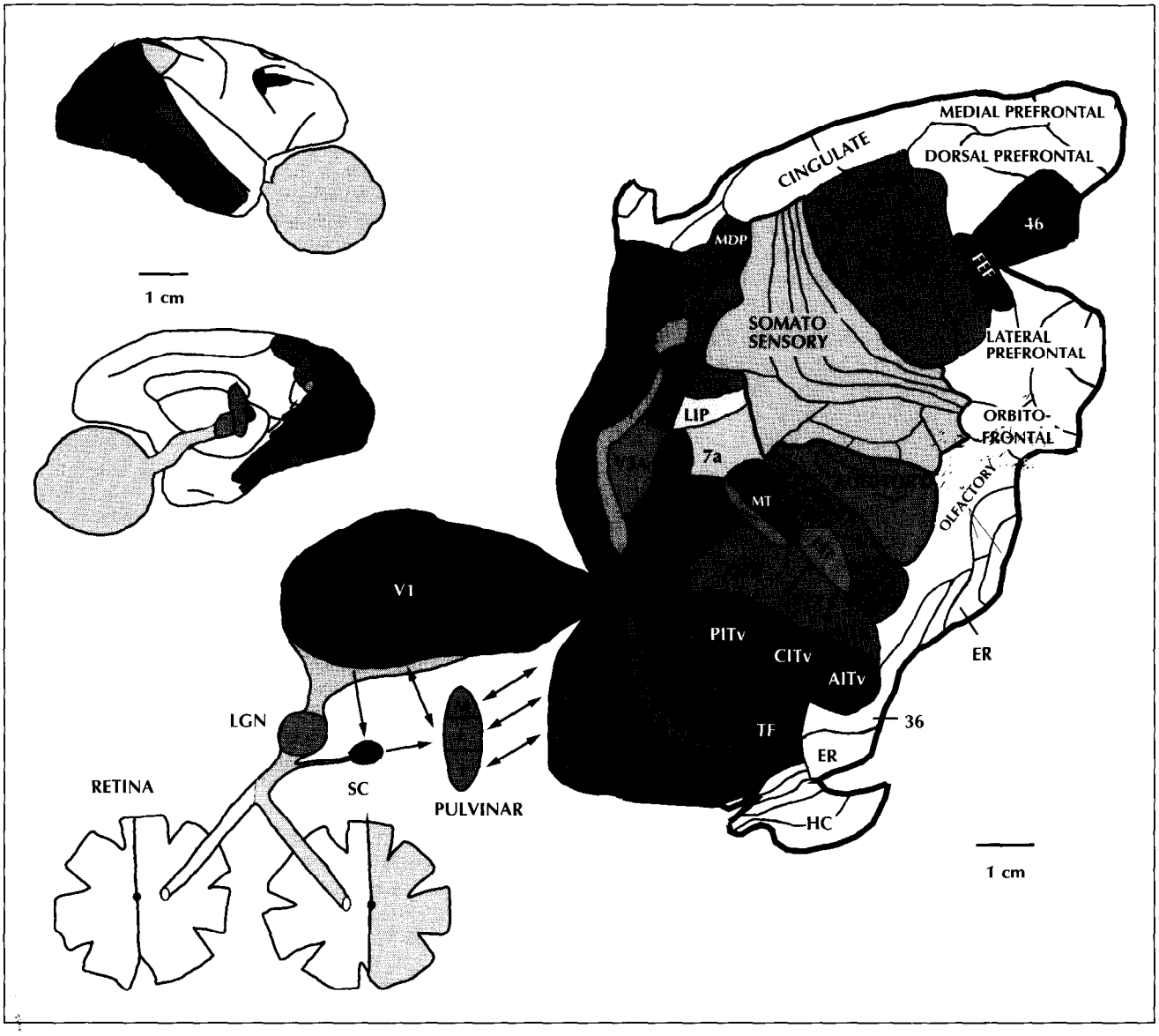

Fig.1 An unfolded two-dimensional representation of visual cortical areas in the macaque monkey, including subcortical visual centers (lower left) and lateral and medial views of the intact brain (upper left). Reproduced with permission from [23].

The identification of visual areas in the human brain is hampered by the obvious restrictions on invasive experimental procedures. Nonetheless, intriguing candidates for homologues of extrastriate areas in non-human primates have arisen from recent anatomical and functional studies. One approach involves the analysis of interhemispheric connections, which are known to preferentially interconnect regions of vertical meridian representation along the borders of several topographically organized areas in monkeys. Clarke and Miklossy [5••] have successfully exploited this arrangement by studying the brains of humans who had unilateral occipital infarcts up to 6 months prior to death. The distribution of degenerating axons in the hemisphere contralateral to the lesion included several callosal-free and callosal-recipient regions similar to those found in monkeys. This analysis, along with a reinvestigation of cytoarchitecture and myeloarchitecture in the same brains, has provided anatomical evidence for putative human homologues of macaque extrastriate areas V2, V3, and VP, along with more tentative candidates for areas V4 and MT.

A complementary physiological approach has involved positron emission tomography (PET) to distinguish cortical regions that are associated with the processing of color and motion [6•]. Subtraction of the regional blood-flow pattern elicited by stimulation with color patterns versus stimulation with non-color patterns resulted in a color-related focus of activity in the vicinity of the fusiform and lingual gyri. Subtraction of responses to moving versus stationary stimuli resulted in a more lateral motion-related focus near the temporo–parieto–occipital junction. While these observations constitute striking evidence for functional specialization within human visual cortex, the identification of response foci with particular visual areas is tenuous. Because of the evidence linking

MT to motion processing [7], the motion-related PET focus was suggested [6•] to be the homologue of macaque MT (V5 in the authors' terminology). However, MT in the macaque is adjoined by other areas (including MSTd and MSTl) that also have a high incidence of direction selective neurons. In addition, the most active region of the motion-related focus appears to be somewhat anterior and dorsal to the location of the putative myeloarchitectonic MT [5••], and it also differs from the motion-related focus reported in a different PET study [8•]. Hence, while it is plausible that the motion-related PET focus includes MT, it may also include (and perhaps even be dominated by) other visual areas as well.

Similar issues apply to the color-related PET focus, which was suggested to represent the homologue of macaque V4 [6•]. The color-related PET focus in humans may well have encroached upon more than one area, especially given that V4 in the macaque is only one of several adjoining extrastriate areas that contain a high incidence of wavelength selective neurons [9,10]. Indeed, multiple color-related foci have been reported in a different PET study involving a color discrimination task [11]. Conversely, physiological and lesion studies strongly implicate V4 in form vision as well as color vision [12]. Along these lines, a PET study using a wider range of test conditions has shown a substantial overlap between foci related to shape processing and color processing [8•]. Thus, while it is tempting to identify activity foci from PET studies as human homologues of specific visual areas of the macaque, corroborating evidence from other anatomical and functional studies must be obtained before these identifications can be made convincingly. The recent development of magnetic resonance imaging (MRI) techniques for monitoring functionally activated changes in cerebral blood flow [13] may help substantially in this regard.

Our ability to extrapolate from monkey to human visual cortex would be improved by a better understanding of the diversity in cortical organization among various non-human primates. Macaques and owl monkeys have been the most intensively studied, but a number of other primates have recently received increased scrutiny, including the squirrel monkey [14,15], the Cebus monkey [16], and the marmoset [17]. Of particular interest is the finding that area DL (a putative homologue of V4 in the macaque) appears to contain multiple subdivisions—three in the owl monkey [18] and two in the squirrel monkey [14]. In the squirrel monkey [14], the caudal subdivision of DL (DL_C) has strong connections with inferotemporal areas and weaker connections with MT, MST, and posterior parietal areas. The more rostral subdivision (DL_R) appears to be at a higher hierarchical level than DL_C and is more strongly linked to MT, MST, and the posterior parietal areas. These distinctions are relevant to the processing streams discussed in the following section.

Concurrent processing streams

Parallel processing streams originate within the retina, where magnocellular (M) and parvocellular (P) classes of retinal ganglion cell convey different types of information about the spatial, temporal, and spectral composition of retinal images. The relative contributions of these two streams to different aspects of visual function have recently been clarified by selective inactivation studies, in which behavioral capacities are assayed after selective lesions of the M or P layers of the lateral geniculate nucleus (LGN). Many tasks can be mediated, at least to some degree, by either the P or the M system acting in isolation. Reductions in contrast sensitivity occur for high temporal frequencies and low spatial frequencies after M lesions, and for low temporal frequencies and high spatial frequencies after P lesions [19•, 20, 21•]. P lesions reduce fine stereopsis but not coarse stereopsis, whereas coarse and fine stereopsis both persist after M lesions [21•]. M lesions raise thresholds for motion detection and discrimination, but mainly for low spatial frequencies and high temporal frequencies; substantial motion discrimination capabilities persist for low temporal frequencies and high spatial frequencies [22•]. One of the strongest differential effects is for color (wavelength) discrimination, which is greatly impaired by P but not by M lesions [19•, 21•]. Visual acuity is also affected by P lesions but not M lesions [19•].

These observations fit reasonably well with the spatiotemporal characteristics reported for P and M cells. They are also in accord with computational arguments that for robust performance, most visual tasks need access to the full range of spatiotemporal information provided by the P and M systems [23]. Some of the results, such as the lack of a pronounced stereopsis deficit produced by M lesions, run counter to previous suggestions regarding the functional specificity of P and M streams [24]. Overall, the segregation of visual processing into two parallel streams may serve to "extend the range of vision, much like rods and cones do for light intensity, with the color-opponent system (P pathway) extending it in the domain of spatial frequency and wavelength, and the broad-band system (M pathway) in the domain of temporal frequency" [21•].

In order for P and M systems to each contribute to a variety of visual tasks, there needs to be anatomical divergence and convergence at appropriate levels of processing. Although there is substantial specificity in the projections of the M and P pathways, significant cross-talk has been demonstrated at several levels in the macaque (see [1••,9]). Substantial cross-talk has also been demonstrated in the owl monkey, where area DM is strongly connected with compartments in V1 and V2 that are associated with both the P and M streams [25].

Tests for cross-talk have also been made physiologically in both MT and V4 following reversible inactivation of P and M layers of the LGN. In MT, pronounced reductions in visually-evoked responses were demonstrated after inactivation of M layers [26•]. After inactivation of P layers, the reductions in MT responsiveness were modest but significant in some cells; it is possible that greater reductions would be found using stimuli whose spatiotemporal characteristics are optimized for P cells. In V4, the inputs appear to be more balanced, insofar as there are pronounced reductions in visual responses after either M or P inactivation (VP Ferrera, TA Nealey, and JHR Maunsell: *Invest Ophthalmol Vis Sci [Abstr]* 1991, 32: 1117). Another distinction between MT and V4 is the degree to

which they are exclusively dependent on the geniculostriate pathway for direct activation. MT receives inputs via the superior colliculus and pulvinar, in a pathway that bypasses the geniculostriate pathway and can weakly drive MT neurons after V1 lesions [27]. In contrast, there is no residual responsiveness in area V4 when V1 is inactivated [28].

At higher stages of the cortical hierarchy, lesion studies have suggested an important distinction between posterior parietal cortex, implicated in the analysis of spatial relationships, and inferotemporal cortex, implicated in object recognition [29]. The degree of anatomical segregation between parietal and temporal lobe streams has been studied using dual tracer injections, with one tracer injected into posterior parietal areas and the other into inferotemporal areas [30•,31]. In general, there is considerable segregation of the inputs to these two regions. Several regions project to both inferotemporal and posterior parietal cortex, however. There is some individual variability in the location and extent reported for these dual projection zones, but they include portions of V4, V3A, DP, the anterior superior temporal sulcus (mainly near the fundus), and perhaps also regions of the frontal lobe that were not examined in either study. The convergence zone in the anterior superior temporal sulcus may be a high level integration site for the different types of processing associated with each stream.

The functional distinction between inferotemporal and posterior parietal cortex has been examined in humans in a PET study involving a face discrimination task and a task analyzing spatial relationships [32]. Both tasks evoked increased blood flow in striate and extrastriate occipital cortex (relative to a sensorimotor control task). In addition, the face discrimination task elicited responses in cortex near the occipitotemporal junction, and the spatial relationship task elicited responses in superior parietal cortex. These observations confirm the functional distinction between human inferotemporal and posterior parietal cortex suggested by lesion studies, and also support previous clinical evidence that the regions of the temporal and parietal lobes specialized for object recognition and spatial relationships, respectively, are displaced relative to their locations in the macaque.

Local circuits

The macroscopic organization of visual cortex discussed thus far provides important constraints on how the system operates, but the actual computations are carried out via the intricate microscopic circuitry within individual areas. Significant advances have been made over the past year in the analysis of specific local circuits, which endow neurons in striate cortex with such basic properties as direction and orientation selectivity, and in the understanding of more complex aspects of receptive field organization.

In the past, efforts to account for specific receptive field properties have often emphasized only one or two mechanisms acting largely in isolation. A classic example is the hypothesis that cortical orientation selectivity arises via convergent excitation from appropriately aligned subsets of LGN afferents [33]. Support for this hypothesis comes from the observation that the receptive fields of LGN afferents converging on any given location of cortex tend to be aligned along an axis correlated with the preferred orientation of cortical neurons at that location [34•]. On its own, however, this mechanism is unlikely to account fully for the sharpness and robustness of tuning for orientation and spatial frequency that is characteristic of many cortical neurons. Other investigators [35,36] have suggested that intracortical inhibition contributes importantly to these characteristics. Intracellular recordings, however, have failed to demonstrate the degree of inhibition predicted by schemes relying predominantly on inhibitory mechanisms [37•].

Recently, a broader synthesis has emerged from a combined anatomical, physiological, and modeling approach applied to the circuitry of striate cortex in the cat [37•–39•,40••]. The puzzling lack of inhibition in intracellular recordings is not attributable to such technical factors as inhibition occurring primarily on dendritic spines or at otherwise electrotonically inaccessible distances from the recording electrode [38•,39•]. Instead, the explanation apparently lies in the delicate balance between positive and negative feedback loops in the local intracortical circuitry. The great majority of excitatory synapses onto cortical cells are from other cortical cells, even in the geniculorecipient layer 4. Douglas and Martin [40••] propose that this intracortical excitation provides the major drive during responses to conventional visual stimuli. In their scheme, LGN inputs activate a local circuit in the cortex, setting in operation a system of feedback loops that ultimately provide the major drive to the cell. With this model, the modest inhibitory potentials recorded intracellularly are sufficient to produce characteristics such as direction selectivity, as they are strong enough to suppress the relatively weak LGN input before it has a chance to set the excitatory intracortical circuitry in action. Circuit-oriented concepts like these may replace the traditional view of the single neuron as the functional unit of cortical processing [41].

Another level of complexity in receptive field organization is the widespread occurrence of modulatory effects arising from outside the classic receptive field (CRF) [42]. For example, the responses of V1 neurons to an optimally oriented bar within the CRF are typically suppressed when the CRF stimulus is part of an overall texture pattern. In addition, the degree of suppression is often greater when the texture field is uniform in orientation than when the CRF stimulus differs in orientation from its neighbors [43]. Under some circumstances, the effects from the far surround can be facilitatory rather than suppressive, and they may even lead to shifts in a cell's preferred orientation [44]. In general, these modulatory influences indicate that responses to visual stimuli depend strongly on the context in which they are presented. One possible anatomical substrate for these surround effects is the long-range horizontal connectivity intrinsic to each cortical area. Intracellular recordings in cortical slice preparations indicate that distant electrical stimulation elicits excitatory postsynaptic potentials whose amplitude can increase several-fold when the postsynaptic cell is depolarized relative to its resting potential

[45•]. This voltage-dependence may explain why stimuli outside the CRF have little effect on a cell's firing on their own, but can have a powerful modulatory role when the CRF is directly stimulated. The fact that distant electrical stimuli evoke inhibitory responses (polysynaptically) as well as excitatory responses may account for the observed mixture of suppressive as well as facilitatory effects.

Conclusion

A theme common to many of the studies cited here is that the visual system is much more complex, at both the system and cellular levels, than was appreciated even a few years ago. This complexity does not arise from sheer perverseness, however. Rather, it is related to the awesome complexity of the computational problems to be solved, and to the flexibility and robustness of the solutions that nature has evolved. Progress in deciphering the function of the visual system will be increasingly dependent upon computational models that capture large portions of the richness of the underlying biology.

References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:
- • of special interest
- •• of outstanding interest

1. •• FELLEMAN DJ, VAN ESSEN DC: **Distributed Hierarchical Processing in the Primate Cerebral Cortex.** *Cerebr Cortex* 1991, 1:1–47.

A comprehensive overview of studies on the anatomical organization of visual cortex, this paper charts the layout and connectivity of known visual cortical areas in the macaque monkey and re-evaluates the hypothesis that the visual cortex is organized as a distributed hierarchy of processing levels.

2. • VAN ESSEN DC, FELLEMAN DF, DEYOE EA, OLAVARRIA J, KNIERIM J: **Modular and Hierarchical Organization of Extrastriate Visual Cortex in the Macaque Monkey.** *Cold Spring Harb Symp Quant Biol* 1990, **55**:679–696.

This paper provides evidence regarding the modular organization of areas V2 and V4, the organization of inferotemporal cortex, and an overview of the overall organization of visual cortex.

3. • BOUSSAOUD D, DESIMONE R, UNGERLEIDER LG: **Visual Topography of Area TEO in the Macaque.** *J Comp Neurol* 1991, 306:554–575.

A physiological mapping study of cortex in and around area TEO. This paper provides important information on the topographic organization of this part of the cortex and also provides evidence for visually responsive neurons in a part of cytoarchitectonic area TF.

4. WEBSTER MJ, UNGERLEIDER LG, BACHEVALIER J: **Connections of Inferior Temporal Areas TE and TEO with Medial Temporal-Lobe Structures in Infant and Adult Monkeys.** *J Neurosci* 1991, 11:1095–1116.

5. •• CLARKE S, MIKLOSSY J: **Occipital Cortex in Man: Organization of Callosal Connections, Related Myelo- and Cytoarchitecture, and Putative Boundaries of Functional Visual Areas.** *J Comp Neurol* 1990, **298**:188–214.

Putative human homologues are suggested for macaque visual areas V2, V3, and VP, and possibly also V4 and MT, based on an analysis of interhemispheric connections and of myelo- and cytoarchitecture in postmortem human tissue. The detailed anatomy provides some of the best evidence to date for the organization of human extrastriate areas.

6. • ZEKI S, WATSON JDG, LUECK CJ, FRISTON KJ, KENNARD C, FRACKOWIAK RSJ: **A Direct Demonstration of Functional Specialization in Human Visual Cortex.** *J Neurosci* 1991, 11:641–649.

A PET study providing evidence for regions of human visual cortex that are specialized for processing different aspects of the visual scene (motion and color).

7. MAUNSELL JHR, NEWSOME WT: **Visual Processing in Monkey Extrastriate Cortex.** *Annu Rev Neurosci* 1987, **10**:363–401.

8. • CORBETTA M, MIEZIN FM, DOBMEYER S, SHULMAN GL, PETERSEN SE: **Selective and Divided Attention During Visual Discriminations of Shape, Color, and Speed: Functional Anatomy by Positron Emission Tomography.** *J Neurosci* 1991, **11**:2383–2402.

A PET study that also shows functional specialization in human visual cortex. Different regions of cortex were preferentially activated when subjects attended to different aspects of a visual stimulus (color, shape, and speed).

9. DEYOE EA, VAN ESSEN DC: **Concurrent Processing Streams in Monkey Visual Cortex.** *Trends Neurosci* 1988, 11:219–226.

10. KOMATSU H, IDEURA Y, KAJI S, YAMANE S: **Color Selectivity of Neurons in the Inferior Temporal Cortex of the Awake Macaque Monkey.** *J Neurosci* 1992, 12:408–424.

11. GULYÁS B, ROLAND PE: **Cortical Fields Participating in Form and Colour Discrimination in the Human Brain.** *Neuro Rep* 1991, 2:585–588.

12. SCHILLER PH, LOGOTHETIS NK: **The Color-Opponent and Broad-Band Channels of the Primate Visual System.** *Trends Neurosci* 1990, 13:392–398.

13. BELLIVEAU JW, KENNEDY DN, MCKINSTRY RC, BUCHBINDER BR, WEISSKOFF RM, COHEN MS, VEVEA JM, BRADY TJ, ROSEN BR: **Functional Mapping of the Human Visual Cortex by Magnetic Resonance Imaging.** *Science* 1991, **254**:716–719.

14. STEELE GE, WELLER RE, CUSICK CG: **Cortical Connections of the Caudal Subdivision of the Dorsolateral Area (V4) in Monkeys.** *J Comp Neurol* 1991, 306:495–520.

15. WELLER RE, STEELE GE, CUSICK CG: **Cortical Connections of Dorsal Cortex Rostral to V II in Squirrel Monkeys.** *J Comp Neurol* 1991, 306:521–537.

16. SOUSA APB, PIÑON MCGP, GATTASS R, ROSA MGP: **Topographic Organization of Cortical Input to Striate Cortex in the Cebus Monkey: a Fluorescent Tracer Study.** *J Comp Neurol* 1991, 308:665–682.

17. DICK A, KASKE A, CREUTZFELDT OD: **Topographical and Topological Organization of the Thalamocortical Projection to the Striate and Prestriate Cortex in the Marmoset (*Callithrix jacchus*).** *Exp Brain Res* 1991, 84:233–253.

18. SERENO MI, ALLMAN JM: **Cortical Visual Areas in Mammals.** In *The Neural Basis of Visual Function.* Edited by Levinthal A. London: MacMillan; 1991: 160–172.

19. • MERIGAN WH, KATZ LM, MAUNSELL JHR: **The Effects of Parvocellular Lateral Geniculate Lesions on the Acuity and Contrast Sensitivity of Macaque Monkeys.** *J Neurosci* 1991, 11:994–1001.

This and [20,21•,22•] explore the contributions of the magnocellular and parvocellular visual pathways to monkeys' perceptual abilities. Lesions of the parvocellular LGN layers caused a decrease in acuity, color contrast sensitivity, and luminance contrast sensitivity in behaving monkeys, whereas magnocellular lesions did not affect any of these abilities except for luminance contrast sensitivity at low spatial frequencies.

20. MERIGAN WH, MAUNSELL JHR: **Macaque Vision After Magnocellular Lateral Geniculate Lesions.** *Vis Neurosci* 1990, 5:347–352.

21. • SCHILLER PH, LOGOTHETIS NK, CHARLES ER: **Role of the Color-Opponent and Broad-Band Channels in Vision.** *Vis Neurosci* 1990, 5:321–346.

This paper reports the effects of magnocellular and parvocellular LGN lesions on a large battery of perceptual tasks in monkeys. Parvocellular lesions impaired color vision, high spatial-frequency form vision, tex-

ture discrimination, and fine stereopsis. Magnocellular lesions impaired high temporal-frequency flicker detection and motion detection. There were no effects of either lesion on low spatial-frequency form perception, coarse stereopsis, and brightness perception, suggesting that both pathways are capable of processing these types of information.

22. • MERIGAN WH, BYRNE CE, MAUNSELL JHR: **Does Primate Motion Perception Depend on the Magnocellular Pathway?** *J Neurosci* 1991, **11**:3422–3429.

Magnocellular LGN lesions affected direction discrimination, but mainly for low spatial frequencies and high temporal frequencies, suggesting a role of both magnocellular and parvocellular systems in motion analysis.

23. VAN ESSEN DC, ANDERSON CH, FELLEMAN DJ: **Information Processing in the Primate Visual System: an Integrated Systems Perspective.** *Science* 1992, **255**:419–423.

24. LIVINGSTONE MS, HUBEL DH: **Segregation of Form, Color, Movement, and Depth: Anatomy, Physiology, and Perception.** *Science* 1988, **240**:740–749.

25. KRUBITZER L, KAAS J: **Convergence of Processing Channels in the Extrastriate Cortex of Monkeys.** *Vis Neurosci* 1990, **5**:609–613.

26. • MAUNSELL JHR, NEALEY TA, DEPRIEST DD: **Magnocellular and Parvocellular Contributions to Responses in the Middle Temporal Visual Area (MT) of the Macaque Monkey.** *J Neurosci* 1990, **10**:3323–3334.

Responses in area MT were substantially reduced by the inactivation of magnocellular LGN layers, whereas the responses were only modestly affected by parvocellular lesions. These results show that MT is predominantly driven by the magnocellular pathway, although a small but significant parvocellular influence is present.

27. RODMAN HR, GROSS CG, ALBRIGHT TD: **Afferent Basis of Visual Response Properties in Area MT of the Macaque. I. Effects of Striate Cortex Removal.** *J Neurosci* 1989, **9**:2033–2050.

28. GIRARD P, SALIN P, BULLIER J: **Visual Activity in Macaque Area V4 Depends on Area 17 Input.** *Neuro Rep* 1991, **2**:81–84.

29. UNGERLEIDER LG, MISHKIN M: **Two Cortical Visual Systems.** In *Analysis of Visual Behavior.* Edited by Ingle DJ, Goodale MA, Mansfield RJW. Cambridge, Massachusetts: MIT Press; 1982: 549–580.

30. • BAIZER JS, UNGERLEIDER LG, DESIMONE R: **Organization of Visual Inputs to the Inferior Temporal and Posterior Parietal Cortex in Macaques.** *J Neurosci* 1991, **11**:168–190.

Dual tracer injections into posterior parietal cortex and inferotemporal cortex show that the inputs to these regions are largely segregated, with only a few areas of cortex projecting to both regions.

31. MOREL A, BULLIER J: **Anatomical Segregation of Two Cortical Visual Pathways in the Macaque Monkey.** *Vis Neurosci* 1990, **4**:555–578.

32. HAXBY JV, GRADY CL, HORWITZ B, UNGERLEIDER LG, MISHKIN M, CARSON RE, HERSCOVITCH P, SCHAPIRO MB, RAPOPORT SI: **Dissociation of Object and Spatial Visual Processing Pathways in Human Extrastriate Cortex.** *Proc Natl Acad Sci USA* 1991, **88**:1621–1625.

33. HUBEL DH, WIESEL TN: **Receptive Fields, Binocular Interaction and Functional Architecture in the Cat's Visual Cortex.** *J Physiol (Lond)* 1962, **160**:106–154.

34. • CHAPMAN B, ZAHS KR, STRYKER MP: **Relation of Cortical Cell Orientation Selectivity to Alignment of Receptive Fields of the Geniculocortical Afferents that Arborize Within a Single Orientation Column in Ferret Visual Cortex.** *J Neurosci* 1991, **11**:1347–1358.

This paper provides evidence for the classic Hubel and Wiesel model of orientation selectivity, insofar as this selectivity may arise in part from the alignment of unoriented receptive fields of LGN afferents.

35. SILLITO AM: **Inhibitory Mechanisms Influencing Complex Cell Orientation Selectivity and Their Modification at High Resting Discharge Levels.** *J Physiol (Lond)* 1979, **289**:33–53.

36. WÖRGÖTTER F, KOCH C: **A Detailed Model of the Primary Visual Pathway in the Cat: Comparison of Afferent Excitatory and Intracortical Inhibitory Connection Schemes for Orientation Selectivity.** *J Neurosci* 1991, **11**:1959–1979.

37. • DOUGLAS RJ, MARTIN KAC, WHITTERIDGE D: **An Intracellular Analysis of the Visual Responses of Neurones in Cat Visual Cortex.** *J Physiol (Lond)* 1991, **440**:659–696.

The first of a series of four papers [37•–39•,40••] addressing the microcircuitry underlying the generation of direction selectivity and orientation selectivity in striate cortex. This paper demonstrates that intracellular recordings fail to detect the strong inhibitory potentials expected from previous pharmacological experiments.

38. • BERMAN NJ, DOUGLAS RJ, MARTIN KAC, WHITTERIDGE D: **Mechanisms of Inhibition in Cat Visual Cortex.** *J Physiol (Lond)* 1991, **440**:697–722.

This paper argues against shunting inhibition as a mechanism that would produce orientation and direction selectivity without producing large changes in the membrane potential.

39. • DEHAY C, DOUGLAS RJ, MARTIN KAC, NELSON C: **Excitation by Geniculocortical Synapses is not 'Vetoed' at the Level of Dendritic Spines in Cat Visual Cortex.** *J Physiol (Lond)* 1991, **440**:723–734.

An anatomical study that rejects the hypothesis that the inhibition occurs by an inhibitory 'veto' at the level of the dendritic spine, a location electrotonically inaccessible to the recording electrode in the soma.

40. •• DOUGLAS RJ, MARTIN KAC: **A Functional Microcircuit for Cat Visual Cortex.** *J Physiol (Lond)* 1991, **440**:735–769.

Proposes a new circuit-oriented model of orientation and direction selectivity involving a combination of positive and negative feedback loops. Modest inhibitory influences are sufficient to generate response selectivity by preventing the activation of positive feedback loops that provide the major excitatory drive to cortical cells.

41. DOUGLAS RJ, MARTIN KAC: **Opening the Grey Box.** *Trends Neurosci* 1991, **14**:286–293.

42. ALLMAN J, MIEZIN F, MCGUINNESS E: **Stimulus Specific Responses from Beyond the Classical Receptive Field: Neurophysiological Mechanisms for Local-Global Comparisons in Visual Neurons.** *Annu Rev Neurosci* 1985, **8**:407–430.

43. KNIERIM JJ, VAN ESSEN DC: **Neuronal Responses to Static Texture Patterns in Area V1 of the Alert Macaque Monkey.** *J Neurophysiol* 1992, **67**: in press.

44. GILBERT CD, WIESEL TN: **The Influence of Contextual Stimuli on the Orientation Selectivity of Cells in Primary Visual Cortex of the Cat.** *Vision Res* 1990, **30**:1689–1701.

45. • HIRSCH JA, GILBERT CD: **Synaptic Physiology of Horizontal Connections in the Cat's Visual Cortex.** *J Neurosci* 1991, **11**:1800–1809.

Distant electrical stimulation can elicit stronger excitatory postsynaptic potentials when the postsynaptic cell is depolarized than when it is at its resting potential. Such voltage-dependent effects may explain the strong modulatory effects of stimuli outside the CRF that ordinarily have no strong influence when presented alone.

David C. Van Essen, California Institute of Technology, Division of Biology 216-76, Pasadena, California 91125, USA.