

Single units and visual cortical organization†

Peter Lennie

Center for Visual Science, and Department of Brain and Cognitive Sciences, University of Rochester, Rochester, NY 14627, USA; e-mail: pl@cvs.rochester.edu

Abstract. The visual system has a parallel and hierarchical organization, evident at every stage from the retina onwards. Although the general benefits of parallel and hierarchical organization in the visual system are easily understood, it has not been easy to discern the function of the visual cortical modules. I explore the view that striate cortex segregates information about different attributes of the image, and dispatches it for analysis to different extrastriate areas. I argue that visual cortex does not undertake multiple relatively independent analyses of the image from which it assembles a unified representation that can be interrogated about the what and where of the world. Instead, occipital cortex is organized so that perceptually relevant information can be recovered at every level in the hierarchy, that information used in making decisions at one level is not passed on to the next level, and, with one rather special exception (area MT), through all stages of analysis all dimensions of the image remain intimately coupled in a retinotopic map. I then offer some explicit suggestions about the analyses undertaken by visual areas in occipital cortex, and conclude by examining some objections to the proposals.

CONTENTS

1 Introduction	889	4.4 Lateral interactions in the domain of spatial structure	907
2 Organizing principles in visual cortex	890	4.5 Summary and assessment	908
2.1 Forming an economical representation	890	5 What is accomplished elsewhere?	910
2.2 Modular analysis	891	5.1 V2	910
2.2.1 Parallel pathways	891	5.1.1 Binocular integration	911
2.2.2 Hierarchical levels	893	5.1.2 Feature linking	913
2.3 Summary and assessment	893	5.2 V3/VP	914
3 Maps and connections in occipital cortex	894	5.3 MT (V5)	914
3.1 The weights of projections	895	5.4 V4	915
3.2 Topography and receptive field size	897	5.5 Summary and assessment	917
3.3 Visual responses of neurons	898	6 Some objections	919
4 What is accomplished by V1?	900	6.1 Separability of perceptual components	919
4.1 Sparse distributed representation	902	6.2 Richness of interconnections	920
4.1.1 How sparse a representation?	903	6.3 Access to consciousness	922
4.1.2 Dimensions of analysis	904	6.4 So little has been achieved	922
4.1.3 Mapping of dimensions	905	7 Concluding remarks	923
4.2 Capturing higher-order structure in the image	906	Acknowledgements	924
4.3 Normalizing for contrast	907	References	924

1 Introduction

Two of the most influential ideas in modern visual science are that the behavior of a single neuron is significant for perception, and that we can infer its role from its visual characteristics—for example, a neuron that responds selectively to the display of a monkey's hand (Gross et al 1972) can be considered a 'hand detector'. The first idea was explicitly and vigorously developed by Barlow (1953, 1972, 1981, 1985):

“Whenever two stimuli can be distinguished, in normal life or in a psychophysical experiment, then proper analysis of the impulses occurring in a *single neuron* would enable them to be distinguished with equal or greater reliability” (Barlow 1985, page 134).

† This paper is developed from ideas first discussed in the *Perception* Lecture delivered to the 16th European Conference on Visual Perception, Edinburgh, 25 August 1993.

The second idea, that the visual properties of a neuron express its perceptual role, is probably in the intellectual baggage of most visual scientists, and motivates a great deal of single-unit recording in visual cortex. We speak casually of a cell being a detector for something (eg a bug), and what I think we mean is that the cell responds best to a stimulus that *looks like* a particular object or attribute of an object. This concept of the visual neuron as feature detector has not often been examined. It is perhaps most explicit in Barlow's (1953) and Lettvin et al's (1959) analyses of receptive fields of the frog's retinal ganglion cells, and in more recent treatments of the properties of neurons in primate inferotemporal cortex (Perrett et al 1987; Desimone 1991; Rolls 1992). It is implicit in many modern electrophysiological studies of single neurons in different visual areas, where the role of a neuron is taken to be the detection of stimuli to which it responds well, and has been especially influential in the development of recent views on functional specialization of visual pathways (Zeki 1978b; DeYoe and Van Essen 1988; Livingstone and Hubel 1988; Zeki and Shipp 1988).

These ideas have been challenged on several grounds. One is that the perceptually significant activity occurs not at the level of the single cell but in groups of neurons (Douglas and Martin 1991; Churchland and Sejnowski 1992). Another is that the visual characteristics of a neuron might provide irrelevant, if not misleading, pointers to its perceptual role (Lehky and Sejnowski 1988). A third is that we generally see surprisingly modest differences among the receptive field properties of neurons in different visual areas. These are troublesome objections to what Douglas and Martin have called the "hegemony of the single neuron". In this paper I examine whether we have been misled by single-unit studies, and whether they have a future. I think the answer to the first question is "slightly", and the answer to the second question is "yes", but these answers need to be developed in the context of a larger view of what visual cortex is doing. In what follows I review a widely held view of visual cortical organization, then I suggest where it needs to be revised, and how single-unit studies can help us evaluate the suggestions.

2 Organizing principles in visual cortex

Two large principles of visual organization draw broad support: first, that the task is to form an economical representation of the visual world; second, that this representation is formed through a modular analysis that is both parallel and hierarchical.

2.1 *Forming an economical representation*

The visual system is widely thought to form a description of the world. Its task is "building a description of the shapes and positions of things from images" (Marr 1982, page 36); "the identification of objects and events" (Treisman 1986, page 35:3); "[to form] a concise description of the three-dimensional scene depicted in the image" (Barrow and Tenenbaum 1986, page 38:2); "to inform us of the identity of objects in view and their spatial positions" (Cavanagh 1989, page 261). The description is complete enough and general enough to support interrogation at many different levels and along different dimensions: from this description we get information about the shapes and positions of objects as well as information about the detail of their surfaces. Two corollary ideas often associated with the notion of a comprehensive representation are that the description is encoded economically, and that it characterizes an object-centered three-dimensional space.

Natural images are readily distinguished from random spatial distributions of color and lightness, and are therefore redundant. The redundancy exists in different forms that have been examined by Attneave (1954), Barlow (1960), Kersten (1987), Field (1987, 1993), Derrico and Buchsbaum (1991), and Atick (1992) among others. By removing it the visual system could transmit information more efficiently—in essence, compress

the image to yield an economical representation that can be analyzed by perhaps fewer neurons or neurons with more limited operating ranges—and might as a result simplify later analysis of the image. Several of the operations undertaken by the retina, for example the center–surround organization of the receptive fields of retinal ganglion cells, which renders them insensitive to spatially uniform illumination, and the transformation of signals from three classes of cones into chromatically opponent signals (Buchsbaum and Gottschalk 1983), can be understood as ways of reducing redundancy in visual signals. Mechanisms in cortex might correspondingly remove some of the more elaborate forms of spatial redundancy that characterize natural scenes (Bossomaier and Snyder 1986; Baddeley and Hancock 1991).

The idea that the representation is object-centered and three-dimensional is perhaps most explicit in the work of Marr (1982) and Biederman (1987). The early stages of visual analysis are thought to give rise to a viewer-centered representation closely coupled to the two-dimensional image on the retina, and higher stages transform this into one in which spatial relations and three-dimensional attributes are represented explicitly.

2.2 *Modular analysis*

Two different sorts of modular organization seem to be present in the visual system. One is represented by parallel pathways for the transmission of information; the other is represented by a hierarchy of stages of analysis.

2.2.1 *Parallel pathways.* It is widely thought that any comprehensive representation of the visual world will be formed through the aggregation of component representations that each carry information about a particular aspect of the image. The kinds of component analyses most often discussed are those that alone might permit the grouping of parts of the image, as a precursor to the segmentation of surfaces in a scene. Among the dimensions suggested for independent analysis are luminance (brightness), texture, color, binocular disparity, movement, and orientation (Barlow 1981; Marr 1982; Livingstone and Hubel 1988; Cavanagh 1989).

The most influential modern evidence for independent analysis of visual attributes comes from physiological and anatomical studies of monkey visual cortex. Although it has been known at least since Holmes (1918) that there are multiple representations of the visual field on cortex, their significance became appreciated only when single-unit recording showed that cells in different areas had distinctively different properties. Dubner and Zeki (1971) and Zeki (1973) found that two anatomically distinct areas in extrastriate cortex, called MT (or V5) and V4, contained a preponderance of neurons that were directionally selective (MT) or chromatically selective (V4). The visual properties of neurons in MT and V4 have since come to exemplify characteristics associated with what are considered to be distinct pathways for the flow of information through cortex (Ungerleider and Mishkin 1982; Young 1992). One pathway, which includes V4, carries information through extrastriate cortex to the temporal lobe. Physiological observations on single units, together with observations on the perceptual effects of damage to this pathway, have suggested that it is, loosely speaking, important for object identification (Livingstone and Hubel 1988; Zeki and Shipp 1988; Merigan and Maunsell 1993). The other pathway, which includes MT, carries information towards parietal cortex, and is considered to be important for the analysis of the movement and positions of objects.

The major pathways contain recognizable subdivisions, and these have been associated with functional differences. Hubel and Livingstone (1987) and Livingstone and Hubel (1988) have made the most explicit suggestion: information about color and shape/orientation of objects is handled by two distinct subdivisions of the temporal system, while information about movement and depth is handled by the parietal system.

What Marr (1982) has called the *principle of modular design* also draws support from other kinds of work. The specificity of visual deficits following accidental damage to different parts of cortex suggests localization of function within modalities (Phillips et al 1984), and a long history of perceptual experiments has demonstrated that different constituents of the image can be handled relatively independently by the visual system (Graham 1989). More recently, experiments that require observers to search for a target among a field of distractors have shown that, depending on the properties of the target and distractors, the search may be effortless and the target immediately identified regardless of the number of distractors, or the search may be slow and require effort of attention (Treisman and Gelade 1980). In cases where the target effortlessly 'pops out' the target and distractors are considered to be handled by different modules, and the pop-out paradigm can be used to identify these (Treisman 1988). Image attributes found to be important here include color, orientation, size, and curvature (Treisman 1986).

Parallel architectures have several attractive properties. Because they permit a computational load to be divided among multiple mechanisms acting concurrently, the result can be obtained faster. Feldman and Ballard (1982) point out that in brains this may be an essential adaptation to having slow computing elements. An obvious expression of this is the sampling of the image by the two-dimensional array of ganglion cells in the retina: the spatial parallelism duplicates a local operation (eg spatial filtering) on the whole image. Although very important, this kind of parallel operation does not bear directly on the *modularity* of perceptual analysis. Parallelism at the level of a module confers a different kind of benefit: if the perceptual problem to be solved has many possible solutions (certainly the case for image interpretation), or there are many ways to solve it (often found to be the case), then the separate computation and reconciliation of different solutions might lead to more reliable and robust decisions (Barrow and Tenenbaum 1978). Encapsulating tasks that can be solved independently may confer the additional benefit that any change in the mechanism that solves one task need have no knock-on effects on the solutions to others (Marr 1982). The analogy here is to organizing computer programs as collections of interconnected functions whose internal workings are substantially private.

Why does modular analysis of the image require several visual maps? A persuasive answer (at least where maps are topographically organized) has two parts: first, perceptual analysis depends on local interactions in the visual field, and these are most economically supported (they will require the shortest connections between neurons) if neurons are arranged so as to preserve the topography of the visual field (Covey 1979; Barlow 1986). Second, if multiple analyses are required (for example, of color, motion, depth), interconnections in a single map between neurons serving the same local region of visual space would be long and perhaps complex, therefore making it economical to ship individual analyses out to their own private maps, within which short connections can be maintained (Covey 1979; Durbin and Mitchison 1990). Barlow (1981, 1986) has developed the argument a stage further: if there is strong pressure against long connections in cortex, then we might expect the neuronal organization underlying fundamental perceptual operations such as grouping to use short connections. Barlow therefore suggested that the linking of common features, which might require associating regions widely separated in space, could be achieved through cortical maps that represent not retinotopic space but some feature space such as orientation or color. To explain a variety of pop-out phenomena, Treisman has postulated similar feature maps (Treisman and Gormican 1988). Young's (1992) analysis of the connections among areas suggests that area 46 and the superior temporal polysensory areas might be major sites of convergence of different analyses.

2.2.2 Hierarchical levels. Different modules can represent not only different *kinds* of analysis, but different *levels* of analysis. Hierarchical organization draws inspiration from the observation that in the macaque the only projection to cortex from the principal laminae of the LGN is to V1 (Wilson and Cragg 1967; Garey and Powell 1971) (so extrastriate areas must depend substantially on inputs from V1) and that within striate cortex one can conceive a hierarchy of neurons with increasingly complex receptive fields (Hubel and Wiesel 1962, 1965). However, the most influential evidence comes from anatomical work showing that known or probable ascending connections originate in the superficial cortical layers and project principally to layer 4, while descending projections originate in the lower cortical layers and project to layers other than layer 4 (Jones and Wise 1977; Rockland and Pandya 1979). Maunsell and Van Essen (1983) exploited this logic to develop a relatively simple road map of cortical organization. Anatomical work in the decade since has added much detail to the picture through the identification of new visual areas and, particularly, the discovery of ever-richer connections among them (Felleman and Van Essen 1991). The known connections among areas do not tightly constrain the structure of the hierarchy (Hilgetag et al 1996), although within occipital cortex it seems reasonably secure.

In a system designed for parallel analysis of the image, hierarchical organization is beneficial because different modules need not duplicate the machinery required for shared components of the analysis (for example, all post-retinal analysis of the image works on a description that has been normalized for overall brightness). This benefit can be expressed through both ascending and descending connections.

The anatomical hierarchy does not, of course, begin in V1; and the lower stages of it, in retina and LGN, have recently attracted considerable attention because they have been thought to provide well-differentiated inputs to different systems of modules in cortex. The anatomical and physiological diversity of retinal ganglion cells and neurons in LGN is well known and well characterized (Rodieck 1988; Lennie et al 1990b; Shapley 1990; Merigan and Maunsell 1993) and has been connected with modularity in cortex by the suggestion (Hubel and Livingstone 1987; Livingstone and Hubel 1988) that the numerically preponderant (P) pathway through the parvocellular division of the LGN drives the temporal stream in cortex, while the (M) pathway through magnocellular LGN provides the major input to the parietal stream in cortex. The P-system is thought to be the precursor of a system that establishes the surface properties and shapes of objects, and the M-system the precursor of a system that establishes movement and depth.

2.3 Summary and assessment

The foregoing account of visual processing glosses over many details and oversimplifies others (particularly the richness of interconnections between different paths through cortex and between different levels in the hierarchy), but one gains from it a picture of consensus among disciplines about the overall design of the system, which we might summarize as follows: the architecture is parallel and hierarchical from the retina onwards; from the LGN onwards the hierarchy carries descending connections as well as ascending ones; in cortex the parallelism increases, within two broad collections of pathways, and there is a concomitant emergence of interconnections between corresponding levels in the different branches; at higher levels in the system retinotopic organization is weak. The different branches analyze information about different fundamental dimensions of variation in the image, and the outcomes of these analyses are later brought together to provide a coherent and comprehensive representation of the forms and positions of objects in the world.

This account leaves unanswered several rather substantial questions: why do we need so many visual areas; why do we need so many stages in the hierarchies of analysis; what is done at each level; how are the outcomes of the different analyses brought together?

In exploring these questions I want to develop the case that the visual system might not work in the way I have just outlined. Rather than undertaking multiple relatively independent analyses of the image from which it assembles a unified representation that can be interrogated about the what and where of the world, *cortex is organized so that perceptually relevant information can be recovered at every level in the hierarchy, that information used for decisions at one level is not passed on to the next level, and, with one rather special exception, through all stages of analysis all dimensions of the image remain intimately coupled in a retinotopic map.* The argument cannot yet be developed rigorously, and weaknesses in it will be evident, but I hope it can be developed reasonably plausibly, and the remainder of this paper is devoted to it.

Although the modular and hierarchical organization in which we are interested begins below cortex, for our present purposes the LGN is uninteresting because the characteristics of neurons in it tell us that (at least in macaque) the representation is fundamentally just a picture of the retinal image, albeit sampled nonuniformly, and normalized to some degree for intensity and color. The representation on cortex is plainly not a picture, and cannot be deduced from the properties of neurons in the magnocellular and parvocellular streams passing through LGN. In what follows I examine the representation in areas in occipital cortex, but not beyond. For occipital cortex one can make the case that useful things are learned whether neurons are studied in anesthetized or awake animals; I am not confident that the same is true for higher visual areas. Moreover, I suggest later that the roles of visual areas beyond occipital cortex differ qualitatively from those of areas in occipital cortex.

3 Maps and connections in occipital cortex

V1 projects directly to at least seven other visual areas (Felleman and Van Essen 1991), and each of these projects to several places. A large projection goes to V2 (Cragg 1969; Zeki 1969), and there is general agreement that this constitutes essentially all the ascending input to V2. Adjoining V2 there are two regions that each contain a representation of a quadrant of the visual field. Because the projections to these regions differ, as do their myeloarchitectures and their receptive field properties, Burkhalter et al (1986) advocated treating them as distinct areas: V3 containing the lower field map and VP containing the upper field map. A simple principle⁽¹⁾ can reconcile all these differences without surrendering the notion that the maps form a single split representation, so I shall refer to the aggregate as V3/VP. V1 sends projections from layer 4B to the lower field representation in V3/VP (Burkhalter et al 1986; Van Essen et al 1986) and to MT (Maunsell and Van Essen 1983). Foveal striate cortex sends a small projection to V4 (Zeki 1978a) and that constitutes a small part of its input. V2 sends major projections to V3/VP, to V4, and to MT. The major ascending projections from V3/VP are to MT and V4 (Zeki 1971). Among the sources of input to MT, that from V2 appears to be strongest (Maunsell and Van Essen 1983).

⁽¹⁾The projection from V1 to V3/VP and MT arises in layer 4B (Maunsell and Van Essen 1983; Burkhalter et al 1986), which is closely tied to inputs from the magnocellular (M) pathway through LGN. The map of the visual field on MT is heavily biased towards the lower temporal quadrant of the visual field (Maunsell and Van Essen 1987) and might well reflect regional variation in the density of M cells in the retina, one aspect of which is a substantial nasotemporal asymmetry in favor of temporal visual field (1.6 : 1 at 4°–8°, rising to 22 : 1 at 50°; Silveira and Perry 1990). If we suppose that the layer 4B output to V3/VP is similarly biased in favor of the lower visual field, we can conceive of V3/VP as a single area, driven principally by inputs from V2, on which a retinotopically biased input from V1 is overlaid. This principle also explains a number of other differences between the upper and lower parts of the representation, and I go into these later. For the moment the useful point is that we can think of the output from layer 4B providing a specialized direct signal whose sampling properties match those of M cells.

3.1 *The weights of projections*

Since connections among areas have been so influential in shaping recent thinking about cortical organization, it would be enormously valuable to know their relative weights, if only to understand what are the major pathways for the flow of information. This is a Sisyphean task, so it is not surprising that anatomical studies provide very little information from which one might estimate the weight of a projection from one area to another, either as a fraction of donor output, or a fraction of recipient input.

We might find qualitative indications of the relative strengths of projections by capitalizing on the principles that cerebral space is very precious and that the metabolic demands of neurons are high. The organization of connections among areas should therefore be such as to minimize the space devoted to fibers. This implies that adjacent and neighboring areas will be the most heavily interconnected, a principle that explains many of the known connections among visual cortical areas (Young 1992). Bearing in mind that cortex is folded in a three-dimensional space, and that the shortest potential connections are not necessarily those implied by the two-dimensional arrangement of areas, the projections from V1, in descending order of size, ought to be to V2, V3/VP, V3A, V4, MT.

We can obtain quantitative estimates of the weights of connections by guessing at more detailed principles underlying their organization. Because extrastriate visual cortex is cytoarchitecturally quite homogeneous (Rockel et al 1980) we can make the simplifying assumption that the density of afferents entering any area is fairly uniform. Suppose, in addition, that the extrastriate areas to which V1 projects reliably and substantially (V2, V3/VP, and MT) receive *all* the output from V1, that each contains a full map of the visual field, and that each assigns to its V1 inputs a weight that reflects the size of V1 in relation to the size of all the other areas that provide ascending input. We are making two separate assumptions: one about the allocation of a donor's outputs among several recipient areas and another about the allocation of a recipient's inputs from several donor areas.

Given these assumptions, we need only know the sizes of the areas (Felleman and Van Essen 1991) to find an upper bound to the fraction of V1 output that goes to each of its recipients. The answer is interesting: V2 receives at most 89%, V3/VP receives at most 8%, and MT receives at most 1%. We can apply the same analysis to the outputs from V2, that is, we assign *all* the output from V2 to the areas to which it projects substantially (V4, V3/VP, V3A, MT) in proportion to their sizes. By this reckoning V4 receives at most 53% of V2 output, V3/VP receives 32%, V3A receives 11%, and MT receives 4%. Likewise, if we assign the output from V3/VP to V4 and MT in proportion to their areas, V3A receives 22%, V4 receives 72%, and MT receives 6%. These estimates are sensitive to the assumption of uniform density of input projections (and might be incorrect for an area, like MT, which has distinctive myeloarchitecture), but are relatively robust to changes in assumptions about the weights placed on connections among areas.

Figure 1 shows this rather limited and much-simplified information in a hierarchical map that provides an unusual picture of visual organization. Visual areas are drawn in proportion to their sizes, and the connections among them shown by lines whose thickness reflects the relative number of fibers involved. Two features are notable. First, the bulk of the information leaving striate cortex is confined to a pathway running through V2 and V4 to the temporal lobe. The preponderance of this stream prompts one to ask whether or not visual analysis really is best conceived as a distributed task, in which the results of different component analyses undertaken separately are ultimately brought together. The arrangement illustrated in figure 1 suggests that much of the analysis undertaken by cortex might be close-coupled, but does not help us understand why some analyses are kept separate. We obtain some clues by considering the kinds

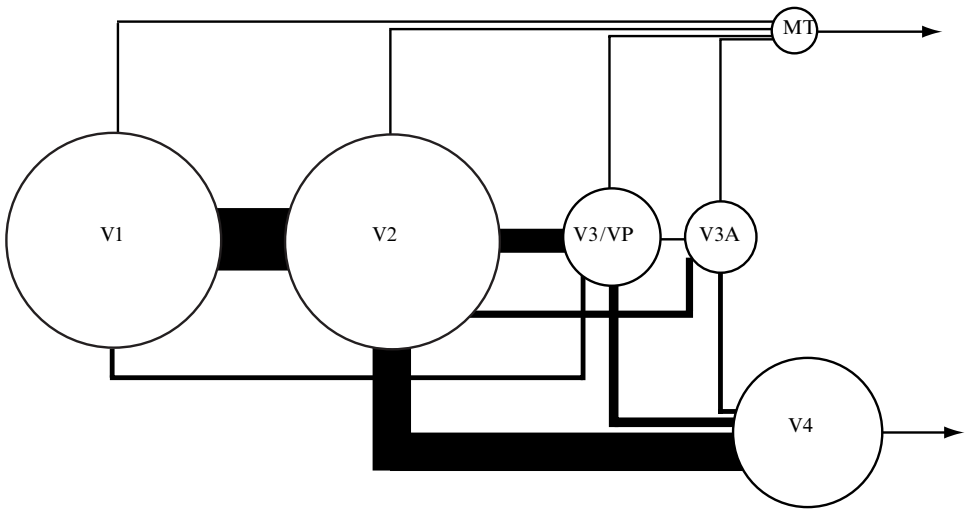


Figure 1. Estimated density of ascending projections among visual areas in macaque occipital cortex. Cortical areas are shown in proportion to their actual sizes, and the thicknesses of lines connecting them are proportional to the numbers of fibers in the pathways. See text for the assumptions on which the estimates depend.

of perceptual tasks thought to be associated with the temporal and parietal streams: the temporal stream is important for the analysis of object properties; the parietal stream is important for the analysis of self-movement. Neither analysis need depend much on the other, and it does not seem necessary that the results of the analyses be brought together later. For example, when one detects and analyzes the flow that results from self-movement, for many purposes it won't much matter what the objects are whose contours contribute to the flow—ignorance of their structure will not impede the analysis (Koenderink 1986). The general organizing principle is that *information is funneled into different pathways only when the ensuing analysis can be self-contained and will lead independently to a perceptual decision.*

The second odd feature of the organization made prominent in figure 1 is that, beyond V2, the maps become progressively smaller as one rises in the hierarchy. Now, this would be easy to explain were the output of one map (eg V2) being fed to multiple destinations whose aggregate areas matched or exceeded that of the source. But that does not happen. No level above V2 has as many cells as V2; no level above V4 has as many cells as that level (figure 2). This implies that a lot of information is discarded at each level in the hierarchy, which in turn implies that perceptual decisions have been made.

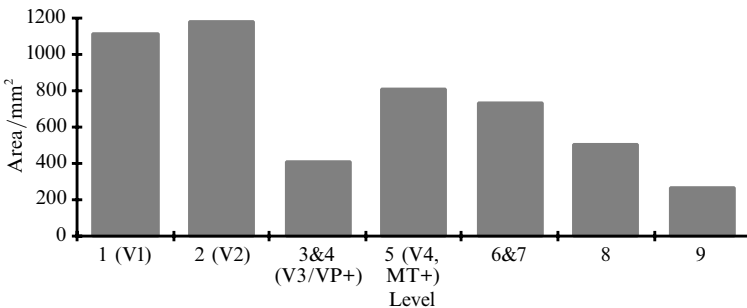


Figure 2. Sizes of visual cortical areas in macaque, aggregated by their levels in the cortical hierarchy. An area's level is determined by the ascending and descending connections it receives from other areas. Based on estimates tabulated by Felleman and Van Essen (1991).

Another organizing principle suggests itself: *perceptual decisions are made at each level of the hierarchy; each level passes to the next the results of its analysis, but not the information used in undertaking the analysis.* On this view, hierarchical organization takes on a new significance: it provides the structure through which the cortex makes perceptual decisions at different levels of complexity.

3.2 Topography and receptive field size

In all extrastriate areas so far examined the topography of the visual field is represented less smoothly than in V1, and with different magnification.⁽²⁾ This has been taken as evidence that retinotopic organization in higher areas is subordinated to a spatially ordered representation of other image attributes (Barlow 1981). Were this so, we might learn about the role of an area by discerning the organization of its map. However, at least in the occipital cortex, the retinotopic organization of extrastriate areas is probably more precise than has generally been supposed, and I think offers little encouragement to the view that the cortical maps are organized for the orderly representation of other attributes of the image.

Hubel and Wiesel (1974), established that in V1 the sizes of receptive fields varied approximately inversely with cortical magnification, with the result that anywhere on the cortical surface one had to move the same distance—about 1 mm—to see a clear shift in the positions of receptive fields (see also Van Essen et al 1984). With this kind of architecture a constant precision in the anatomical connections within cortex will be expressed as a larger scatter of receptive field positions as magnification decreases. In V2 the magnification factor is slightly lower than in V1, and the map quite precise (Gattass et al 1981), which is perhaps not surprising given their similar surface areas. In the other extrastriate areas, which are a good deal smaller, the magnification factor near 1° eccentricity is much lower than in V1: in V3/VP (~ 20% of the area of V1) the magnification factor is perhaps 3–5 times less (Gattass et al 1988); in V4 (~ 50% of the area of V1) the magnification factor is 2–3 times less (Maguire and Baizer 1984; Gattass et al 1988); in MT (~ 5% of the area of V1) the magnification factor is 5–10 times less (Albright and Desimone 1987; Maunsell and Van Essen 1987). If, as seems likely, the underlying architecture of the extrastriate areas follows V1 in the precision of its local connections, we would expect the lower magnification factors to result in greater apparent disarray in the positions of receptive fields, being greatest in V4 and (especially) MT. This is exactly what has been found, but it does not imply any weakness in the retinotopic organization of the areas—indeed in V4, small lesions bring about retinotopically precise impairments of vision (Merigan 1996).

The gross comparison of magnification factors in different areas overlooks interesting local differences among areas, for the maps of the visual field are not all replicas of the one in V1. By comparison with V1 the map on MT overemphasizes the peripheral visual field (Albright and Desimone 1987) and hugely overemphasizes its lower temporal quadrant (Maunsell and Van Essen 1987); in contrast, the map on V4 seems to underrepresent the peripheral visual field (Gattass et al 1988).

The receptive fields of neurons in extrastriate areas are larger than in V1, often substantially so. At corresponding eccentricities near the fovea receptive fields in V2 are (in linear dimensions) 2–3 times larger than in V1 (Gattass et al 1981; Foster et al 1985); in V3/VP 4–5 times larger (Felleman and Van Essen 1987; Gattass et al 1988); in V4 perhaps 5–6 times larger (Maguire and Baizer 1984; Desimone and Schein 1987; Gattass et al 1988); in MT 7–10 times larger (Albright and Desimone 1987; Maunsell and Van Essen 1987). The expansion of receptive fields bears an interesting relationship to the magnification factor. This is easy to see if we take the ratio of receptive field size

⁽²⁾The magnification factor is the distance on the cortical surface that contains the representation of 1 deg visual angle.

to magnification factor, and normalize that ratio to the value found in V1 (figure 3). For V2 this normalized ratio is ~ 2.5 , for V3/VP ~ 1.251 , for V4 ~ 2.2 , and for MT ~ 1.13 . These numbers are, of course, very rough, but they tell us something rather important: in V2 and V4, but not in V3/VP and MT, receptive fields cover the visual field more densely than they do in V1, and are larger than they need to be to compensate for any difference in magnification. This suggests a substantial investment in machinery for spatial integration.

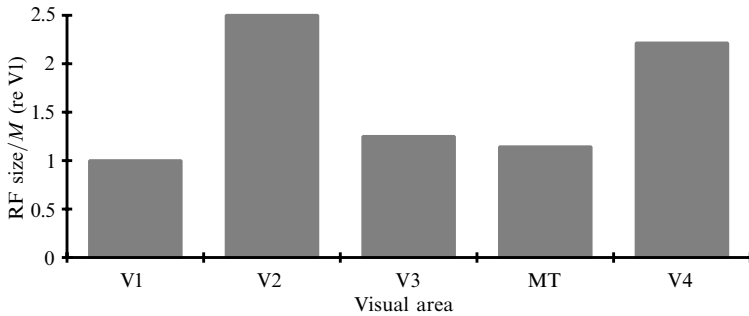


Figure 3. Ratio of average receptive field (RF) size to magnification factor M , for the central visual field (about 1° eccentricity), in different areas of macaque occipital cortex. This ratio is calculated separately for each area, then normalized to the ratio found for V1. Calculations were made with the use of the following values for magnification factor, averaged from sources given in the text: V1: 7.5 mm deg^{-1} ; V2: 4 mm deg^{-1} ; V3: 2 mm deg^{-1} ; V4: 2.6 mm deg^{-1} ; MT: 1.5 mm deg^{-1} .

3.3 Visual responses of neurons

Observations on the visual sensitivities of neurons tell us surprisingly little about the functions of the different areas. The most impressive thing about occipital areas other than MT is that, by the tests commonly used to explore receptive fields, neurons behave remarkably similarly, all having characteristics broadly like those of cells in V1. Figure 4 (based upon Felleman and Van Essen 1987) captures well what I mean.

A summary as compact as figure 4 does of course obscure interesting differences among areas, and I shall discuss some of these below, but the difficulty of finding truly distinctive differences among the properties of neurons in different areas draws attention sharply to the question of whether individual cells are well characterized by the techniques we use to study them, or differ in interesting ways that we have not yet captured. We can learn something about this from the capacity of different stimuli to drive cells. Although it is sometimes hard to find any stimulus that will drive a cell effectively, most neurons in extrastriate cortex can be excited well by some stimulus in the limited repertory of the experimental physiologist, discharging 50 or more extra impulses per second; some respond reliably to weak stimuli that might be in the threshold range for human vision. There is little doubt that for many neurons we have found quite effective stimuli, if not the best ones. This is surprising if one takes the view that cells at higher levels of the visual pathway should have progressively more elaborate stimulus requirements, and it might make one pessimistic about the future of single-unit physiology, for it implies that the important functional differences among visual areas will not be expressed at the level of the single cell. I think this is too skeptical a position, but it does serve as caution to physiologists not to confuse an adequate stimulus with an optimal one, and it highlights the importance of knowing what to look for when characterizing neurons.

We discover one rather important principle by looking at the relationship between the contrast of a stimulus and the response of a cell. In the parts of the visual pathway where it has been examined, the relationship between the response of a cell, R , and

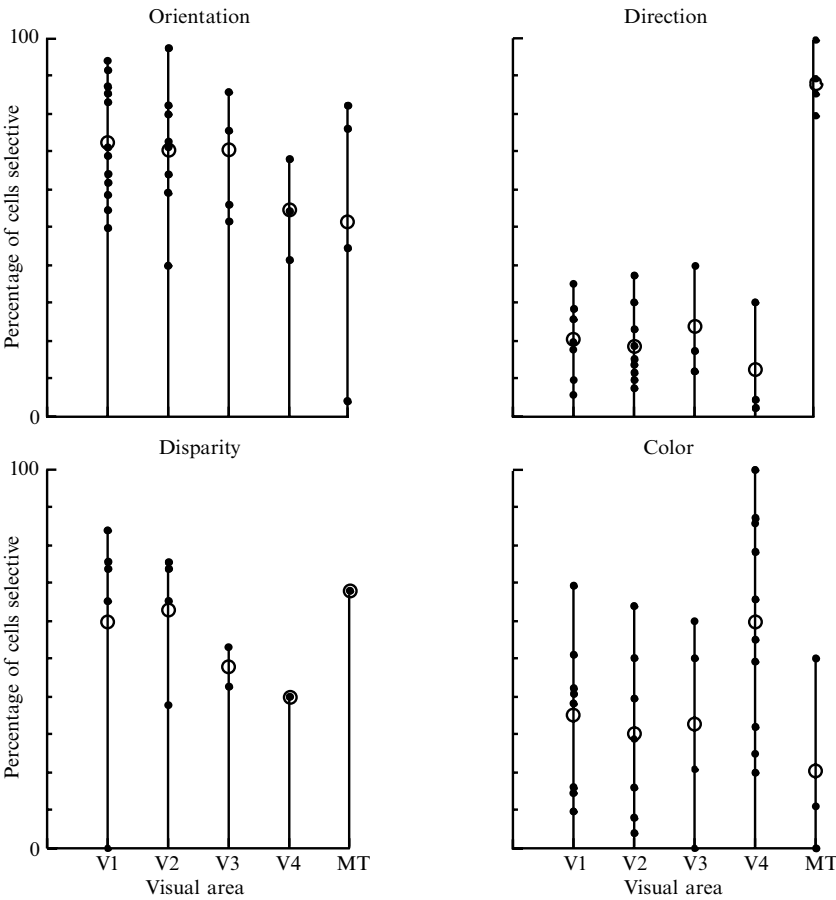


Figure 4. Estimates of the proportions of neurons in different visual areas that respond to stimuli designed to test the selectivity of cells for orientation, direction of movement, binocular disparity, and color. Each filled point represents an estimate from a single study; the open circles show the unweighted averages. Most values shown are taken from Felleman and Van Essen (1987), who provide sources; estimates from some later studies (Desimone and Schein 1987; Saito et al 1989; Schein and Desimone 1990; Levitt et al 1994; Gegenfurtner et al 1997; Kiper et al 1997) have been added.

the contrast, c , of its preferred sine-wave grating is reasonably well described by the function

$$R = R_{\max} \frac{c^n}{(c^n + c_{50})}$$

The three parameters R_{\max} , n , c_{50} , characterize respectively the maximum response, the slope of the rising part of the curve, and the gain or sensitivity. As one moves up the visual pathway from one level to another, n becomes progressively larger (figure 5); that is, the curves become much steeper (Sclar et al 1990).

Cells therefore become, in the contrast domain, progressively more like switches, being either on or off; their dynamic range is not used. A steep relationship between contrast and response tends to make neurons very selective for visual stimuli (a point developed by Geisler and Albrecht 1995), and *the progressive steepening of contrast – response relationships at higher levels in the pathway implies increasingly sharp selectivity for visual stimuli, purchased at the expense of the capacity to signal variations in contrast.*

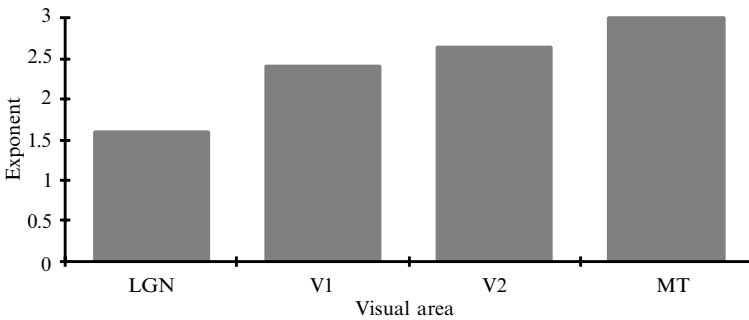


Figure 5. Steepness of the relationship between stimulus contrast and response amplitude, for neurons at different levels in the visual pathway. The slope increases with level.

The foregoing discussion has suggested some general principles of organization, but it has not taken us far towards understanding the distinctive things different areas do. Moreover, it suggests that, in the absence of some larger view of what cortex is doing, single-unit recordings are unlikely to provide the insights we seek. To make progress we need to consider which tasks might reasonably be accomplished by V1, and which are left to be dealt with by higher areas.

4 What is accomplished by V1?

The distinctive properties of receptive fields in V1 are well-known, following the work of Hubel and Wiesel (1962, 1965, 1968) and later investigators. What is less well understood is why cells have the properties they do, and why there are so many of them. The enormous number of neurons in macaque V1—O’Kusky and Colonier (1982) estimate more than 2×10^8 in each hemisphere—is more than 200 times the number of fibers leaving the eye (400 times if one counts a pair of on-center and off-center ganglion cells as a unit), and provides around 200 000 cells per hypercolumn, which we might provisionally consider to be the functional unit for image analysis (Hubel and Wiesel 1974). Put simply, there are perhaps 400 times as many neurons as would be needed to represent all the information conveyed by the LGN. Even if we look only at layers II and III, which send outputs to other regions of cortex, there are still 100 times more cells than would be needed.

We can pursue (and emphasize) this point by asking a slightly different question: how many cortical neurons would be needed to represent all the spatial and chromatic detail we can see in an image? The answer is probably “many fewer neurons than are contained in the LGN”. One way to find out is to examine encoding schemes that can represent the image economically. This has been most thoroughly pursued in the domains of spatial frequency and orientation, where it appears that sparse arrays of oriented local filters with spatial characteristics of the kind possessed by ganglion cells and simple cells in V1 can very compactly encode as much information as a human observer can extract from the image of a static scene (eg Watson 1987, 1990). This sort of result encourages the notion that the *purpose* of the neurons in V1 is to construct an economical description of the image. That idea also draws support from work that has inferred the properties of mechanisms that might be capable of extracting the principal components of variation in the spatial structure of natural images. Principal components analysis packs variance in the image into the smallest possible number of basis functions, so mechanisms that can extract the principal components ought to be able to represent the image compactly. Bossomaier and Snyder (1986) and Hancock et al (1992) have drawn attention to the similarity between some of the principal components of natural scenes and cortical receptive fields. Derrico and Buchsbaum (1991) have shown

that, when the analysis is extended to include the chromatic structure of scenes, the major components resemble the spatiochromatic receptive fields of neurons in striate cortex.

Data compression through redundancy reduction does seem to be an important result of early transformations undertaken in the retina—particularly those that discard information about absolute intensity while retaining information about contrast, and those that transform cone signals into chromatically opponent ones (Srinivasan et al 1982; Buchsbaum and Gottschalk 1983; Atick 1992). Some additional redundancy is surely removed in V1, as Barlow (1972) first suggested: one clear expression of this is the generally more transient responses of cortical neurons to continuously presented stimuli. But, if producing a compact representation is principally or even substantially what V1 does, why do we find, in moving to V1 from LGN, a tremendous increase rather than a reduction in the number of cells? Even if we impose additional requirements, for example that the representation combine information from two eyes to encode surface depth, it seems unlikely that providing for that could account for the vast number of neurons. [There is in fact little binocular integration in macaque V1, a point I return to later. Moreover, Powell and Hendrickson (1981) observed that cortex representing the binocular and monocular parts of the visual field cannot be distinguished anatomically, and that in both a unit of visual field is represented by the same number of neurons.] We have to consider that V1 might be doing nothing like producing a compact, complete representation of the image.

Barlow (1981) suggested that a large number of neurons might be required for spatial interpolation during image reconstruction, thereby providing our capacity for fine spatial discrimination, but there seems to be no need for such mechanisms, for one can establish relative location quite precisely with spatially selective mechanisms that are themselves coarse (Watt and Morgan 1984). Indeed, Shapley and Victor (1986) have demonstrated that even the cat's ganglion cells, which have much larger receptive fields than those in primate, nevertheless provide signals from which relative location can be computed very precisely.

The key to understanding what V1 is doing may lie in an entirely different direction. The fundamental job of the visual system must be to analyze images so that the observer can *classify* objects quickly and reliably—most crudely as things already known, or things unknown. A binary decision obscures the richness and complexity of classification—such as our remarkable capacity to characterize degrees of likeness among objects (even unknown ones), and to classify them by different rules on demand—but it draws attention to the problem, which is how to relate sensory information to stored knowledge of the world, and to find the concordances and discrepancies. Knowledge of the world is continually being revised, and how this is done is a fundamentally important problem, but I think not the one to focus on in trying to understand V1, for there is little reason to believe that in the adult the normal organization and function of V1 show any long-term susceptibility to experience.⁽³⁾ The more appropriate question might be: how should the image be analyzed so as to facilitate classification? Pursuing this provides some insight into the number of neurons in V1.

⁽³⁾ Some recent evidence suggests that a scotoma resulting from a retinal lesion eventually provokes reorganization of the topographic map in V1, associated with a reduced representation of the scotoma (Kaas et al 1990; Heinen and Skavenski 1991; Gilbert and Wiesel 1992). There is little reason to suppose that this kind of reorganization reflects a general capacity of adult striate cortex to change its properties with experience. Long-term restrictions or peculiarities of the visual diet of adult monkeys do not discernibly affect visual function (Harwerth 1986). On the other hand, short-term changes in sensitivity and tuning ('habituation' or 'adaptation') that depend on the recent history of visual stimulation (Vautin and Berkley 1977; Movshon and Lennie 1979; Sclar et al 1989) could lead one mistakenly to conclude that receptive fields on the edge of a scotoma had encroached upon it (DeAngelis et al 1995).

4.1 *Sparse distributed representation*

The classification problem faced by the visual system is one of a broader set of much-studied problems in associative memory: given an enormous set of possible objects, how can sensory information (often incomplete and noisy) be used to retrieve, quickly and reliably, the object that most likely corresponds to it? The notion of *most likely* is important here, for visual signals will rarely be consistent with only one interpretation. Workable/interesting solutions to this problem have exploited what is in essence table lookup: the sensory information is examined by an array of analyzing mechanisms whose responses provide the values on a multidimensional input vector (Ballard 1986; Hinton et al 1986). The sensory decision is represented by the distribution of activity in an array of output mechanisms to which the input mechanisms are connected with specified weights. The question of how weights come to be properly specified, so that inputs are correctly mapped to outputs, is important but not immediately relevant to the present discussion. What is important here is that simple networks that associate multidimensional input and output vectors can generalize well, in that similar input vectors give rise to similar output vectors, and they are robust: they can deliver the most likely output vector from an incompletely specified input vector. A distributed representation in which a given sensory element contributes to the encoding of multiple objects can also store potentially many more objects than there are elements in the network (Churchland and Sejnowski 1992).

The properties that endow distributed representations with high capacity, and permit them to generalize usefully, also make them vulnerable to the problem that in color vision is recognized as metamerism: different input vectors can give rise to the same output vector. One way to minimize this is to organize the network so that any single object is represented by activity in only a small subset of the network elements (Willshaw 1981; Kanerva 1988). In the limit, a sparse representation has a single object represented by a single element, and becomes a representation of the kind familiar to physiologists: a single neuron is the detector for a particular object (eg ‘grandmother’).

The general consequences of different degrees of sparseness are easily summarized: the greater the number of network elements that participate in the representation, the better the network will generalize, but the more readily it will confuse different input vectors. Moreover, the activity of an individual element will provide a progressively poorer indication of the nature of the object represented—knowing about a neuron’s receptive field will provide a poor indication of its perceptual role. In a very sparse representation, generalization is poor, but the potential for misclassification is reduced, and the activity in the individual element more directly reflects the characteristics of the object represented.

Quantitative studies of single neurons in striate cortex show them to be remarkably heterogeneous in their selectivities on image dimensions such as spatial frequency, orientation, chromaticity, and direction of movement. The heterogeneity in the domains of spatial frequency (De Valois et al 1982a; Hawken and Parker 1987) and orientation (De Valois et al 1982b) led Robson (1980) to suggest that V1 encodes the image as orientation and spatial frequency vectors—a distributed representation. Sakitt and Barlow (1982), Watson (1987, 1990), and Daugman (1988) have developed these ideas quantitatively, suggesting particular arrangements of mechanisms for efficiently covering the perceptually useful space of orientation and spatial frequency. Is this kind of representation sparse, in that a natural object will give rise to activity in only a small subset of neurons?

The intensity variations in natural scenes have distinctive amplitude and phase spectra. The amplitude spectrum falls approximately inversely with frequency (Burton and Moorhead 1987; Field 1987; Tolhurst et al 1992), and the phase spectrum is highly structured: in particular, within a given region of the frequency spectrum the phases

at different frequencies tend to be aligned (Field 1993). Significant features, such as edges, where the phase will be aligned on different scales, can be relatively easily discovered by spatial filters of the kind represented by cortical receptive fields (Marr and Hildreth 1980; Morrone and Burr 1988). Moreover, Field (1993) has shown that natural scenes will be sparsely represented by mechanisms with receptive fields of the kind possessed by simple and complex cells: the spatial bandwidth of a single cell—on the order of 1.5 to 2 octaves—is such as to capture the region of the spectrum over which phase is coherent. Field (1994) has also shown for simulated neurons that a bandwidth of around 2 octaves would give rise to the sparsest distribution of responses to natural scenes.

The argument developed so far is that a sparse distributed representation provides robust storage and easy retrieval of information, and that the properties of neurons in V1 facilitate a sparse representation of natural scenes. Sparseness might be desirable for other reasons too. The metabolic cost of action potentials is high,⁽⁴⁾ so, as Baddeley (1996) points out, there must be strong pressure to keep spike traffic to a minimum. The cost of a silent neuron is perhaps a hundred to thousandfold lower, so there are incentives to develop a representational system that minimizes the number of action potentials at the expense of requiring a large number of neurons.

In developing the case for a sparse representation, a number of important issues have been glossed over, among which are: (1) How sparse should the representation be—what balance is to be struck between the need for generalization and the need for precision in classification? (2) What might be the dimensionality of the representation in cortex? We have so far considered a vector that encodes a range of orientations and a range of spatial frequencies, but normal scenes vary also in color and depth, and objects move. (3) How might the different dimensions of analysis be represented in the anatomical organization of cortex?

4.1.1 *How sparse a representation?* This is a question of practical as well as theoretical importance, for the answer determines the properties that physiologists will seek when studying the receptive fields of neurons. In the sparsest possible representation a single element represents a single stored object. To the extent that we identify an element with a neuron, its receptive field properties will resemble the object stored when the representation is very sparse, but need bear little resemblance when the representation is dense. Experimental observations suggest that in V1 the representation cannot be very sparse, for it is easy to observe, with single-unit (or grosser) recording methods, that any stimulus that drives a single cell well actually excites many neurons.

Can the representation be organized in a way that provides the storage capacity and generalization benefits of distributed representation without the risk of misclassifying visual objects? In this connection mechanisms of color vision are of some interest, for the broad spectral tuning of the three classes of cones permits an unlimited number of input spectral distributions to evoke identical outputs from the three types of receptors. In practice, however, the spectral characteristics of natural surfaces are drawn from a small part of the space of possible ones, and few *natural* surfaces will give rise

⁽⁴⁾Very roughly, the generation and propagation of a single action potential in the brain might involve the transport of 3×10^8 sodium ions (probably more). The Na^+/K^+ pump that maintains/restores ionic balances draws its energy from the hydrolysis of adenosine triphosphate (ATP) to adenosine diphosphate (ADP). During hydrolysis, each molecule of ATP moves 3 Na^+ . The adult human brain consumes about $0.25 \text{ kcal min}^{-1}$ —about 20% of the energy used by the body (Clarke and Sokoloff 1994). Of this, between 20% and 40% is consumed in the hydrolysis of ATP to ADP, which yields about 12 kcal mol^{-1} (Albers et al 1994). For the whole brain this corresponds to a movement of about $1 \times 10^{22} \text{ Na}^+ \text{ min}^{-1}$. If we suppose (unrealistically) that spike generation and propagation account for all the energy used by the pump, the total consumption supports round $5 \times 10^{11} \text{ spikes s}^{-1}$ —no more than a few spikes per second per neuron, and perhaps considerably less.

to confusable signals in cones (Maloney 1986). Is there any corresponding organizing principle in the larger domain of visual objects that permits the economies of distributed representation but ensures that natural objects would be confusable only with objects that do not exist in nature? There seems to be no evidence on the matter, but an interesting conjecture is that *the representation in V1 will be just sparse enough to ensure that there are few metamers in the domain of natural objects*. For man-made images we need have no such expectation, and it might be productive to view some visual illusions as the expression of metameric confusions arising from the image analysis undertaken by visual cortex.

4.1.2 Dimensions of analysis. A distinctive feature of the multidimensional analysis under discussion is that a single neuron occupies a place on each of the dimensions along which the image is analyzed. This notion is at odds with the view, argued by Livingstone and Hubel (1988), that different dimensions of variation in the image are segregated for analyses. On that view, an abstract signal about a particular dimension is extracted from the input. It is not really clear what might constitute such an abstract signal, but for movement it could be something like an unstructured motion flow field. In the case of color, the implicit though seldom articulated notion is that a 'pure' chromatic mechanism lacks orientation and spatial selectivity—it has some amorphous receptive field sensitive only to color variations. The main point is the expression of sharp selectivity for only one stimulus dimension. This is not typical of neurons in V1. Consider, for example, directionally selective cells that might be the beginnings of a pathway specialized for analysis of movement. These generally have sharp orientation and spatial selectivity (De Valois et al 1982b; Orban et al 1986). Not even in the layers of striate cortex that are the probable sources of outputs to area MT (Hawken et al 1988), or even in individual cells that project to area MT (J A Movshon, personal communication) does one find receptive fields like those of 'pure' directionally selective neurons in the rabbit's retina (Barlow et al 1964). There seems to be equally little sign of a 'pure' chromatic mechanism. Although such a mechanism would be easy to construct from LGN inputs (D'Zmura and Lennie 1986), different investigators who disagree about many aspects of the physiology of color vision (Livingstone and Hubel 1984a; Thorell et al 1984; Tootell et al 1988a; Ts'o and Gilbert 1988; Lennie et al 1990a), do agree that chromatically opponent neurons often have spatially complicated receptive fields.

Physiological observations make it perfectly reasonable to suppose that an individual neuron in V1 occupies a place on many dimensions along which the image is analyzed, and a good deal of psychophysical evidence on contingent aftereffects points to the same conclusion.⁽⁵⁾ The best-known example is the McCollough effect (McCollough 1965; Skowbo et al 1975), but there is an abundance of other evidence for multidimensional analysis. For example, Bradley et al (1988) showed that the orientation and spatial selectivities of contrast aftereffects are tied to the chromatic properties of the adapting stimulus; Cavanagh (1989) and Flanagan et al (1990) showed that tilt aftereffects of opposite sign could be induced concurrently by using gratings that were defined by variation along different dimensions, such as color or texture.

One can imagine this kind of architecture extended to include yet other dimensions of variation in a scene, for example depth. It would, however, be comforting if we had some principled way of establishing the dimensions of analysis. Adelson and Bergen (1991) observed that a seven-dimensional description of the visual world is sufficient, with the distribution of intensities in it expressed as a function of wavelength, time; x and y position in the image plane; and X , Y , and Z position of the viewer. The Y and Z axes can be sampled only by changing the position of the head, so at any moment the visual system can sample five dimensions of the image. Because natural images are redundant

⁽⁵⁾ See Graham (1989) for a discussion of the logic (and potential weaknesses) of such experiments.

in all dimensions, their structure can be captured economically by recording low-order derivatives on the fundamental dimensions (Watson 1990). Adelson and Bergen (1991) point out that to capture even one-dimensional first-order and second-order derivatives, and separable and oriented two-dimensional ones, a large number of measurements are needed at any point. We might therefore think of a hypercolumn in V1 containing the machinery to represent some of the more important one-dimensional and polydimensional derivatives of the image on the x and y directions in the image, the X dimension of the viewer's position (disparity), wavelength, and time. Given about 200 000 neurons per hypercolumn the image might be analyzed along five dimensions or derivatives with about eleven sample points per dimension. There is, of course, no reason to suppose that all dimensions of variation are sampled equally densely (for color only three samples are taken, for disparity two, and for time there are perhaps only two or three sampling mechanisms), but the important point is that multidimensional analysis quickly consumes large numbers of neurons.

4.1.3 *Mapping of dimensions.* How is a multidimensional analysis packed into V1? For the dimensions of X and Y position, orientation in the coronal plane and (possibly) position in depth, a clear answer was provided by Hubel and Wiesel: a map that preserves the overall retinal topography is tessellated locally by eye of input, and within eye by the preferred orientation of neurons (Hubel and Wiesel 1977). Mitchison (1991) has shown this arrangement to be economical when neurons make most of their connections locally in a domain (eg for one eye) but must make some elsewhere in the domain (the other eye). Other dimensions or derivatives could be incorporated by extension of the same principle, through further subdivision of the map in the X – Y plane, or vertically.⁽⁶⁾ If V1 does contain a multidimensional map of the image organized by nested tessellation, the mapping of deeply nested dimensions could be hard to discern because a small movement through cortex will result in a substantial progression along a dimension. Nonetheless, for some candidate dimensions there are hints of orderly representation.

Tootell et al (1988b) found, by analyzing the uptake of the metabolic marker ¹⁴C-2-deoxyglucose, that low spatial frequencies preferentially excited cells in the 'blob' regions of V1 that are rich in cytochrome oxidase, and lie as patches in the middle of ocular dominance columns (Horton and Hubel 1981); higher spatial frequencies preferentially excite cells outside blobs. There is disagreement on the existence of any more finely ordered representation of spatial frequency (Silverman et al 1989; Born and Tootell 1991). There might also be an ordered representation of chromaticity, though the evidence is less clear. Vautin and Dow (1985) and Ts'o and Gilbert (1988) (though not Lennie et al 1990a) saw some columnar specialization for color—Vautin and Dow by primary hue (red, yellow, green, blue), Ts'o and Gilbert by opponent system (red-green, yellow-blue)—but no one has found clear signs of a continuous representation. In fact, a contrary organization is implied by the observation (Livingstone and Hubel 1984a) that the cells best excited by chromatic contrast, and which are apparently rarely orientation-selective or size-selective, are concentrated almost exclusively in the blobs, which thus appear to disrupt an otherwise orderly mapping of ocular dominance and orientation selectivity.

How blobs fit into the cortical map is of some importance, for the view that they are part of a distinct functional subsystem (Livingstone and Hubel 1984a; 1988) is inimical to the position for which I have argued here. More recent evidence suggests that blobs are probably not part of a special subsystem. The distribution of orientation

⁽⁶⁾This argument ignores the possibility that some dimensions of image variation might be encoded in the temporal fine-structure of the discharge of neurons. The structure of the discharge does contain some information about the visual stimulus (Optican and Richmond 1987), but it is not clear that in the visual system the timing of action potentials is precise enough to permit a rich representation of the kind suggested by Hopfield (1995).

preferences over an extended region of cortex, inferred from images of intrinsic signals in cat area 18 (Bonhoeffer and Grinvald 1991) and monkey V1 (Blasdel 1992), shows frequent discontinuities where different progressions of preferred orientations collide. The discontinuities are probably a general feature of cortical organization; they emerge through the coordinated development of orderly and economical arrangements of orientation selectivity and ocular dominance from initially undifferentiated states (Durbin and Mitchison 1990; Swindale 1992) and are therefore very much part of the normal map. In macaque these discontinuities lie on the blobs (Blasdel 1992), and we might suppose the same to be true of other primates that show similar patchy distributions of cytochrome oxidase in V1. What remains to be explained is why chromatically opponent neurons should be concentrated on the discontinuities in the orientation map. A good deal of recent evidence suggests that they are not (Tootell et al 1988a; Lennie et al 1990a; Leventhal et al 1995); those in blobs may be more easily discerned simply because they prefer stimuli of low spatial frequency and are readily excited (Edwards et al 1995).

4.2 *Capturing higher-order structure in the image*

One of the most striking physiological differences between LGN and cortex is the presence in V1 of neurons with complex receptive fields. These receptive fields lack discrete excitatory and inhibitory regions, instead having a structure characterized as a collection of subunits, each of which has a local spatial organization much like the receptive field of a simple cell, and whose outputs are rectified then summed, causing complex cells to be excited by local contrast regardless of its sign or position within the receptive field (Movshon et al 1978; Spitzer and Hochstein 1985). Complex cells discard information about the nature of the local features in the image, so it is important to understand why this is valuable.

One of our more powerful perceptual capabilities is to capture, often effortlessly, the extent of regions of common structure (texture) in the image without necessarily, or at least not without effort, being able to specify the local features that define the structure. Robson (1980) first suggested that complex cells might be well suited to encoding the attributes of textures, and mechanisms with the rectifying properties of complex cells, which capture the general but not the particular characteristics of local structure, are prominent in modern treatments of the discriminability of textured patterns (Bergen and Adelson 1988; Bergen and Landy 1991; Graham et al 1993). Complex cells (though generally not simple cells) respond well to textures (Hammond and MacKay 1977) and to similar local changes in image structure (Nothdurft and Li 1985; Grosf et al 1993).

This conception of the role of the complex cell—as providing a token that captures the general characteristics of the local structure in the image—leads to other insights on the organization and function of V1. First, to the extent that it is important in early vision to extract general characteristics of a local region [in Adelson and Bergen's (1991) terms, 'stuff' rather than 'things'] we might expect to find cells that respond not just to 'amount of local contrast' but perhaps also to 'amount of movement' or 'amount of color'. For V1 the evidence is equivocal: some complex cells clearly are selective for the direction of stimulus movement, but direction selectivity is not often a conspicuous attribute (De Valois et al 1982b; Hawken et al 1988); complex cells also respond to chromatically modulated stimuli (Lennie et al 1990a), but not in a way that suggests the extraction of some general signal about 'amount of color'. Second, if we view the complex cell's description of local structure as a prerequisite to finding regions of common structure, we recognize that what the complex cell achieves in the domain of texture much simpler mechanisms do in the domain of color: given the nature of the signals arriving from LGN almost no work needs to be done to encode a local region of uniform color.

This is probably why so little of the machinery in V1 seems to be concerned with representing color. Third, since we have conscious access to the details of the local image structure that complex cells discard, much of the information analyzed by simple cells must find its way out of V1 without passing through complex cells (simple cells are also found in V2).

Although complex cells in V1 provide an important initial stage in characterizing higher-order structure in local regions of the image, the perceptually significant operation is the discovery of common structure in a region. This requires, if not the explicit recognition of adjacent areas of common structure, the recognition of boundaries at which structure changes. In either case lateral interactions are implicated, so it is worth examining whether V1 might be involved in the discovery of regions.

4.3 *Normalizing for contrast*

It has recently become clear that an important stage in producing the sharp spatial and orientation selectivity of V1 neurons is an expansive nonlinearity (following some linear combination of signals from LGN) that generates steeply accelerated curves relating response to stimulus contrast (Albrecht and Geisler 1991; Bauman and Bonds 1991; Heeger 1992a). This exacerbates a problem already present for many cortical neurons, namely that the limited response range of the cells, culminating in saturation, makes it hard to maintain high sensitivity to contrast (and sharp orientation and spatial selectivity) over any sizable range of contrasts. The problem is in some ways like that caused by the wide range of illuminations over which the visual system has to operate, and dealt with by retinal mechanisms of light adaptation: these discard information about the absolute level of illumination and leave a ganglion cell's operating point and sensitivity set for the ambient illumination, so that response amplitude depends largely on the local contrast in the image (Enroth-Cugell and Shapley 1973; Derrington and Lennie 1982). In a broadly analogous way V1 seems to preserve the sensitivity and selectivity of cells over a wide range of contrasts by a mechanism of contrast adaptation or inhibition that adjusts the sensitivity and operating point of the cell to some weighted average of the local contrasts in space and time (Robson 1988; Heeger 1992b). These mechanisms, which are not orientation-specific and seem to be confined to the classical receptive field, have been explored most thoroughly in the cat (Morrone et al 1982; Ohzawa et al 1985; Bonds 1989, 1991; DeAngelis et al 1992). It is not clear that they are as important in the monkey, where V1 neurons seem to have lower contrast sensitivity and generally need less protection against saturation (Sclar et al 1989, 1990).

4.4 *Lateral interactions in the domain of spatial structure*

Within V1, horizontal processes that can extend over 6 mm or more make connections in regularly spaced patches with a period that matches one cycle in the map of preferred orientations (Gilbert and Wiesel 1983; Rockland and Lund 1983). The connections seem to be relatively specific: cells in blobs in macaque V1 are connected to cells in nearby blobs but not to cells in intervening regions (Livingstone and Hubel 1984b), and in cat V1 (though not V2—Matsubara et al 1987) connections are made preferentially between regions having the same preferred orientations (Gilbert and Wiesel 1989). Some long-range connections in macaque V1 are made on smooth interneurons, and are probably inhibitory; many are made on the dendrites of pyramidal cells and are presumed excitatory (McGuire et al 1991). Moreover, to the extent that one can discount common inputs, cross-correlation of responses recorded from neurons in places separated by the period of connections suggests excitatory transmission between them (Ts'o et al 1986; Ts'o and Gilbert 1988), although does not exclude inhibitory ones.

The existence of presumed excitatory long-range connections has encouraged the idea that they provide a means for the mutual reinforcement of responses to the same local structure at neighboring places in the visual field, and thereby support the spatial

integration of information that must underpin such fundamental perceptual operations as detecting extended contours and linking regions of common spatial structure. This might be accomplished in different ways. Long-range connections might give rise to synchronizing signals that help establish the relatedness of different regions excited by matching stimuli (Singer 1993). Gray et al (1989) and Engel et al (1991) have suggested that a resonance near 40 Hz sometimes seen in the responses of neurons in cat V1 might be especially helpful in establishing figural continuity among neighboring regions of visual field. Recent evidence showing that these oscillations can originate in the cat's retina (Ghose and Freeman 1992, 1997) weakens the case that they depend on long-range connections in cortex; moreover, in monkey even the existence of resonant firing is controversial (Young et al 1992; Livingstone 1996).

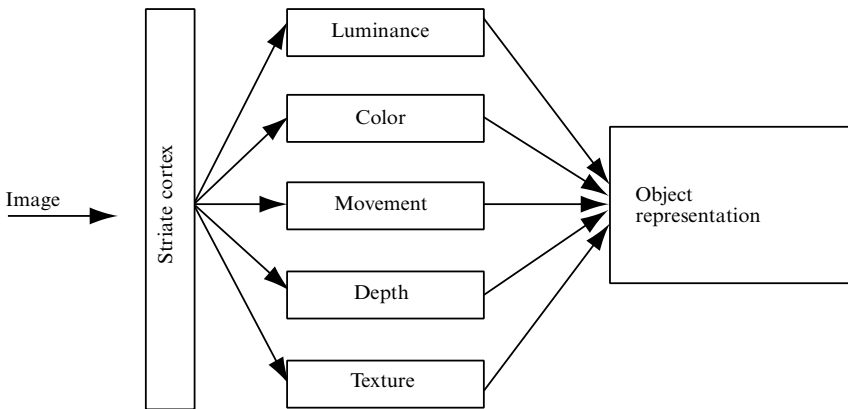
Another means by which long range connections could facilitate linking is through direct reinforcement of responses among interconnected neurons with similar stimulus preferences (Gilbert 1992). The V1 receptive field is usually characterized as the region within which stimulation controls the cell's discharge directly; beyond it there is often a zone where stimulation modulates the response to a stimulus in the receptive field, but cannot itself evoke a response. Excitatory influences accumulated from surrounding zones have been found in cat (Maffei and Fiorentini 1976; Nelson and Frost 1985; Gilbert and Wiesel 1990) and in monkey (Sillito et al 1995; Müller et al 1996; Levitt and Lund 1997), but are rarely (cat) or never (monkey) such that stimuli of like orientation reinforce one another. In monkey especially, patterns of *contrasting* structure on the receptive field and the surrounding region are required for facilitation. In both cat (Maffei and Fiorentini 1976; Blakemore and Tobin 1972; Nelson and Frost 1978) and monkey (Lamme 1995; Levitt and Lund 1997) when a neuron is excited by a stimulus in the receptive field a similar stimulus in a surrounding region enclosing the receptive field generally suppresses the discharge. The more similar the stimuli in the two regions, the greater the suppressive effect of the surround (Gulyas et al 1987; Zipser et al 1994; Levitt and Lund 1997).

The behavior when stimuli fall on the receptive field and on the region surrounding it has been interpreted as revealing a mechanism for segregating figure from ground (Orban et al 1987; Lamme 1995), or a mechanism that facilitates perceptual 'pop-out' (Knierim and Van Essen 1992). However, for reasons elaborated later, I believe these are higher-level operations than could reasonably be undertaken by V1. Spatial interactions in V1 probably have a less exotic role: they provide lateral inhibition in the domain of local structure, so that, by analogy with lateral inhibition in the luminance domain, signals from regions of common structure are suppressed and contrasts in structure are made salient.

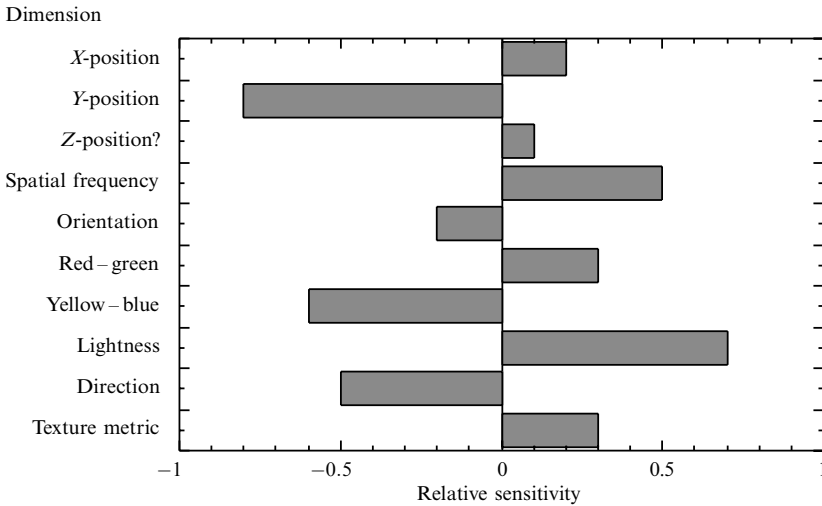
4.5 Summary and assessment

The argument is that, rather than transforming inputs to yield parallel output streams, in each of which cells carry information about a single dimension of the image and are largely indifferent to variations in other attributes, the output from V1 is a multi-dimensional vector, with each cell occupying a defined place on multiple dimensions. Figure 6 contrasts these views diagrammatically.

From the point of view of the single-unit physiologist, a caricature of the difference is that by the first model we might expect to see a population of color-coded cells responding well to variations in color, but largely indifferent to variations in the other attributes of the image, while by the other we might expect cells to have well-defined preferences on each of the dimensions along which distinct attributes of the image are analyzed. I think physiological evidence favors the second model and anatomical evidence is consistent with it, both in terms of the expansion of cell numbers and in their arrangement. Moreover, the kind of organization it represents is known to have



(a)



(b)

Figure 6. Contrasting views of information transmission through cortex. (a) Information about different attributes of the image is analyzed relatively independently: V1 separates information about the different dimensions and dispatches it to different extrastriate regions each specialized for a particular kind of analysis. At a later stage, the results of the different analyses are combined. (b) V1 preserves, in a closely-coupled relationship, all the information about different dimensions of the image. Each neuron in V1 is most sensitive to a small region of a multidimensional space, and its properties can be represented by a multidimensional vector, shown diagrammatically here. The abscissa represents the relative sensitivity of the neuron to stimuli on each of the dimensions identified in the ordinate.

properties desirable in a classifier: similar input vectors give rise to similar output vectors, and it can deliver the most likely output vector from an incompletely specified input vector. Finally, an architecture that uses huge numbers of neurons, most of which can be silent most of the time, could be a valuable adaptation to the high cost of generating spikes.

V1 also undertakes an important analysis, expressed in the behavior of complex cells, that captures local structure in the image. It also normalizes signals for contrast so that the information passed on to other areas is relatively independent of the absolute level of contrast in the image. And it removes (or at least reduces) redundant signals about extended regions of common structure. One might think of V1 as transmitting *decisions* (albeit about elementary attributes of the image) to higher cortical areas, but perhaps little of the information that gives rise to these decisions.

5 What is accomplished elsewhere?

I have promoted a view that ascribes to V1 an elaborate analysis of the image, and one might ask whether too much is imputed to it, and too little left for other areas to do. It is perhaps worth emphasizing that V1 in macaque contains almost as much raw machinery as all the other recognized visual areas combined. V1 in macaque constitutes about 20% of visual cortex by area (Felleman and Van Essen 1991), but because (uniquely to primates, and largely as a result of the organization of layer 4) the density of neurons there is 2.5 times greater than elsewhere in neocortex, which is otherwise quite uniform (Rockel et al 1980), V1 contains about 40% of all visual neurons. V1 probably contains all the machinery required to account for psychophysical performance on a range of fundamental perceptual tasks—the detection of contrast patterns in brightness or color, the discrimination of orientation and spatial frequency (Vogels 1990; Zohary 1992), and some of the perceptual hyperacutities (Parker and Hawken 1985)—and there seems to be no good reason to look beyond it to explain them. Many important tasks are left for higher areas. We require mechanisms that can support binocular single vision, since V1 in monkey apparently does little to combine information from the two eyes. We need mechanisms for establishing continuity and detecting structural similarities that span substantial distances, even intermittently, for V1 cannot have got far in solving this ‘linking’ or ‘binding’ problem. We require mechanisms for detecting higher-order structure such as symmetry and for assigning boundaries to surfaces. We also require mechanisms for analyzing the translations and deformations of the visual field (optic flow) that accompany movements of the eyes and/or body.

5.1 V2

V2 is at least as large as V1, and, with the exception of what might be regarded as special projections from layer 4B of V1 to V3/VP and MT, is the conduit for essentially all visual cortical information. Most neurons in V2 are orientation-selective (Zeki 1978d), though perhaps slightly less sharply so than cells in V1 (Levitt et al 1994); their preferred spatial frequencies are a little lower (Foster et al 1985), but in most respects neurons in V1 and V2 are not remarkably different (Baizer et al 1977; Hubel and Livingstone 1987), having broadly the same mix of directional selectivities and similar distributions of chromatic preferences. Several of the candidate dimensions for image analysis seem to be explicitly represented on the retinotopic map in V2. The most conspicuous organizing principle is that cells with common preferences tend to be clustered (DeYoe and Van Essen 1985; Shipp and Zeki 1985; Livingstone and Hubel 1988). For example, in a region 500 μm or more in diameter the cells might all prefer similar orientations (Hubel and Livingstone 1987; Tootell and Hamilton 1989). On a large scale the mapping of orientation seems to be complicated, for there are elongated regions (‘stripes’) running across the width of V2, among which there are clear variations in the proportions of cells that are orientation-selective. Anatomical markers identify three kinds of stripes (thick, thin, pale, named for their appearance when stained for cytochrome oxidase) that extend across the width of V2, with the triplet repeating cyclically along its length (Tootell et al 1983). Orientation-selective cells are common everywhere, but more so in the thick and pale stripes than in the thin ones; direction-selective cells are common though not preponderant in the thick stripes, but rarer in the thin stripes and pale stripes; color-selective cells (often not orientation-selective) are found most often in the thin stripes, but nowhere predominate; cells that prefer binocular stimulation are most often found in the thick stripes (DeYoe and Van Essen 1985; Shipp and Zeki 1985; Hubel and Livingstone 1987; Peterhans and von der Heydt 1993; Levitt et al 1994; Gegenfurtner et al 1996). Tootell and Hamilton’s (1989) observations suggest that there might also be some systematic mapping of spatial frequency.

The patchy organization and clustering of cells with like selectivities is what one might expect were V2 organized to maintain a vectorial analysis of the sort I suggested was made by V1: each cell has a defined position on several dimensions along which the image is analyzed, and the clustering reflects the optimal packing of the analysis into the two-dimensional cortical sheet (Durbin and Mitchison 1990). However, the observations do not point very firmly to vectorial analysis, and, coupled with anatomical evidence that cells in the thin and thick stripes project differentially to V4 and MT respectively (DeYoe and Van Essen 1985; Shipp and Zeki 1985), have been used to argue a different view, namely that information about different dimensions of the image is segregated in distinct pathways embodied in the stripes (Livingstone and Hubel 1987; Roe and Ts'o 1995). I think the arrangement must be more complicated than this. A triplet of stripes spans a distance of 4 mm or more, which for macaque fovea represents more than 0.5 deg of visual angle. This is a surprisingly coarse functional unit when we consider that a hypercolumn in V1 spans 1 mm, in fovea representing about 0.1 deg. Some finer-scale organization presumably remains to be discovered. We know that cells preferring similar orientations, and perhaps also cells preferring similar spatial frequencies, do occur in V2 in clusters on a scale of around 0.5 mm, but we don't know the arrangement of clusters representing different orientations or different spatial frequencies, and we know nothing at all about local organization for other dimensions of analysis.

Part of the difficulty in understanding local organization in V2 probably stems from the fact that we have not discovered what it does—how it augments the analysis undertaken in V1. Although the moderately tight retinotopy of the map implies an analysis that emphasizes local interactions in the 2-D image plane, the things V2 does seem to be relatively subtly expressed in the behavior of single cells, whose properties generally differ little from those of neurons in V1. Two characteristics of V2 neurons—their binocularity and their receptive field sizes—do give us pointers.

5.1.1 *Binocular integration.* Neurons in macaque V1 can often be driven through either eye, but rarely are the two eyes equally effective (Hubel and Wiesel 1968). The way in which a V1 neuron combines signals from the two eyes has not been explored thoroughly in macaque, but in cat the work of Ohzawa and Freeman (1986a, 1986b) shows it to be quite linear in simple cells and about half of complex cells: within limits, the binocular response is approximately the sum of the responses that would arise from stimulation of either eye alone. Although the physiological and anatomical prominence of ocular dominance columns in macaque points to relatively fewer neurons than in cat being readily driven by either eye, there is no reason to suppose that the rules of binocular combination differ in the two species. The general consequence of these rules is that although a neuron might be driven well through only one eye, or through either eye alone, for it to be driven well through both eyes together stimuli must be relatively precisely matched and relatively precisely aligned. The upshot is that, with an effective stimulus in one eye, a slight binocular mismatch can markedly affect the response of a cell, but a gross mismatch will have little effect. Neurons in V1 might therefore be viewed as providing a filter that permits relatively unhampered monocular vision, but exerts strong constraints on the binocular signals that will be combined.

The foregoing discussion bears only indirectly on the special qualities of binocular vision, namely the extraction of depth from disparity (stereopsis) and the properties of binocular single vision. The former has been much studied, and it is clear that binocularly driven neurons in V1 could provide a substrate for stereopsis, either through their two receptive fields being horizontally misaligned (Barlow et al 1967; Poggio and Fischer 1977) or through the two receptive fields having different structures

that make them sensitive to stimuli in different spatial phases (Freeman and Ohzawa 1990; DeAngelis et al 1991).⁽⁷⁾

Binocular single vision has received very much less attention than stereopsis, but it certainly cannot be less important, and must depend on complex underlying processes. Because the images in the two eyes are generally disparate over much of the visual field, the singleness of vision we enjoy must result from some fusion of the images or the suppression of one. Both processes seem to be at work. Fusion is proven by the observation that images of an object falling on non-corresponding points occupy different visual directions when seen with either eye alone, but, when seen with both, occupy a single intermediate direction. Suppression of one eye's image is readily demonstrated when two very different images fall on corresponding regions of the retinas. Both fusion and suppression must depend upon quite elaborate analysis of the features in the monocular images rather than upon simply establishing point-by-point correspondence, for the range over which fusion occurs depends critically on the nature of the patterns (Braddick 1979), and when one eye suppresses the other it predominates not only in spatially coherent units, but to some degree synchronously for units that have common features (Whittle et al 1968).

The processes underlying suppression and fusion are largely untouched by physiologists (though see Poggio et al 1988; Sengpiel et al 1995; Lehky and Maunsell 1996; Leopold and Logothetis 1996). The suppression of signals from one eye in binocular rivalry is widely thought to require mechanisms that are specified for eye of input, and has been taken to implicate V1 (Blake 1989), yet the complexity of the interactions revealed psychophysically, and their coherence over sometimes large spatial range, are not easily reconciled with what we know about the behavior of neurons in V1. Moreover, the observations that grossly mismatched stimuli in the two eyes generally interfere little in binocular cells (Ohzawa and Freeman 1986a, 1986b) and that V1 neurons respond well to a stimulus that is perceptually suppressed (Leopold and Logothetis 1996) suggest that the site might be elsewhere. Fusion of different images requires mechanisms that are disparity-tolerant, and these are not characteristic of V1. These considerations prompt one to explore a different view of rivalry and suppression: that they originate at a higher level in the visual pathway, where cells might be indifferent to the eye of origin of their inputs.

The binocular properties of V2 neurons differ in several ways from those of V1 neurons. Almost all neurons in V2 are excitable through either eye or both together and, unlike neurons in V1, most are equally excitable through either eye (Hubel and Wiesel 1970; Burkhalter and Van Essen 1986). This is reflected in the anatomical organization of V2, which shows no sign of the ocular dominance columns that are such a distinctive feature of V1 (Tootell and Hamilton 1989; Ts'o et al 1990). Some of the binocularly driven neurons—investigators disagree on the fraction, though probably less than half—are disparity-selective, and respond best to concurrent stimulation of the two eyes by precisely positioned stimuli (Hubel and Wiesel 1970; Poggio and Fischer 1977), but most seem indifferent to whether they are driven by either eye alone or both together over a broad range of phases (Hubel and Livingstone 1987). This tolerance of misalignment hints at a mechanism for binocular fusion, and points to a remarkable but discreet transformation of visual signals that takes place between V1 and V2: *the representation in V2 is not only fully binocular, but cyclopean, and V2 might be considered the site of binocular single vision.* If V2 has discarded information about eye of origin, it has no way of knowing when signals from the two eyes are in conflict, and therefore has no way of knowing that it would be beneficial to suppress signals from one eye. One interesting possibility is that what underlies binocular rivalry is

⁽⁷⁾Cumming and Parker (1997) provide interesting evidence that disparity-selective neurons in macaque V1 do not provide reliable cues to depth.

not principally the selection of an eye for suppression but the selection of a *stimulus* for suppression. This kind of selection, for which Logothetis et al (1996) provide some evidence, could be made at a high level (in V2 or beyond), and a signal to suppress information about particular *stimuli* could be propagated back to V1 where, if images in the two eyes differ, it results in the suppression of information from one eye.

Some gross indication that V2 is important for binocular fusion might be obtained by simple measurements, on cells that are well-driven by either eye, of the neurons' tolerance of differences in stimulation of the two eyes—how is the response to the preferred stimulus in one eye affected by the presentation of a differently oriented or differently colored stimulus in the other? The more interesting perceptual aspects of fusion and suppression imply cooperative interactions that find similar (but not identical) image features in the two eyes, and in this connection it would be interesting to know whether V2 cells are sensitive to disparity gradients of the kind that define local changes in surface shape.

5.1.2 *Feature linking.* Neurons in V2 and V1 are sharply distinguished by the sizes of their receptive fields. Larger receptive fields in V2, coupled with the greater overlap of receptive fields implied by figure 3, might provide part of a mechanism for establishing continuity of local structure across regions of the image, and for underpinning the binocular integration we have just discussed. Barlow (1981) suggested that extrastriate visual areas might be involved in establishing linkages between features, but the mechanism he envisaged—maps organized in a feature space (eg, color represented in the manner of a chromaticity diagram) rather than a retinotopic one—is quite unlike the one considered here, and for areas in occipital cortex is, I think, precluded by their retinotopic regularity.

Most of the observations we have on the properties of V2 neurons are not well-suited to revealing a role in feature integration, and new kinds of experiments might be required to understand it. For example, were a large receptive field organized to detect collinearity it might be more sensitive to the relative offsets of pattern elements within the receptive field than to the absolute position of a single element that spanned the length of both. The cell would nonetheless respond well to the single bar, which is of course what we find. One can imagine analogous experiments to examine the specificity of linking in other domains, eg how do differences in the structure of two separated texture elements affect summation within the receptive field, or how does a cell respond to disjunctive movement of elements within the receptive field? How does a cell summate signals when presented with, say, a green grating of low spatial frequency in one part of its receptive field and a red grating of higher spatial frequency in another part? Although no one seems to have undertaken experiments of quite this kind, Peterhans and von der Heydt (1989) have described cells in V2 that do reveal a remarkable and very nonlinear integrative mechanism that can combine information from line segments across gaps of 2 deg or more. Moreover, von der Heydt and Peterhans (1989) show that this mechanism can accommodate perceptual elements more complex than just lines. In the domain of binocular integration one might expect to see signs that cells often care more about similarities in the *structure* of the stimuli falling on the two eyes than they do about similarities in the *positions* of the stimuli.

We now have some pointers to what V2 might do: it finds local similarities in image structure that are used to support binocular single vision and at least short-range perceptual grouping along any dimension of stimulus variation. It is important not to underestimate what is accomplished by V2. Almost all of the output from striate cortex passes through it, and damage to it might be expected to produce greatly impaired vision. Where this has been looked at in humans, in cases where one can exclude damage to striate cortex though not damage to V3, patients seem to be virtually blind (Penfield

and Rasmussen 1950; Horton and Hoyt 1991). It therefore might be thought surprising that, in monkeys, circumscribed lesions of V2 markedly impair performance on tasks that require grouping of discriminable elements but have no effect on local discriminations of luminance, color, and orientation (Merigan et al 1993). The observations on human and monkey may not be very difficult to reconcile. One can imagine that the analysis undertaken by V1 would permit reliable simple discriminations on forced-choice tasks, without this giving rise to conscious seeing.

5.2 V3/VP

V3/VP is the most enigmatic of the occipital areas, because its cells generally lack distinctive visual characteristics, and because its outputs are directed principally towards regions (V4 and MT) that already receive much of their input from V2. The characteristics of receptive fields in the upper and lower parts of the representation are similar, but cells with different sorts of visual preferences occur with different frequencies. Orientation-selective cells are common in both divisions, though they appear to be less selective than neurons in V2 (Baizer 1982); directionally selective cells are common in the lower field representation (Zeki 1978c; Felleman and Van Essen 1987; Gegenfurtner et al 1997) but not in the upper field map (VP). This difference can be readily explained by supposing that the map of the lower field receives much more direct input from layer 4B of V1. Color-selective cells are relatively frequent (Burkhalter and Van Essen 1986; Felleman and Van Essen 1987; Gegenfurtner et al 1997); the population of neurons that are both color-selective and direction-selective seems to be distinctive (Gegenfurtner et al 1997). Many neurons appear to be sensitive to binocular disparity (Felleman and Van Essen 1987; Poggio et al 1988)

On the whole, single-unit work tells us little about what V3/VP does, and it might be more profitable to try to understand it by considering some of its gross properties and by analyzing the flow of information to it and from it. Although we can say little about the details, its relatively small size and large receptive fields imply a coarse analysis. The intermediate position of V3/VP also makes it likely that signals from it reach V4 and MT later than do signals from V2. These observations, coupled with the fact that V3/VP apparently provides only a small fraction of the input to V4 and MT suggests that its role might be *to provide a spatially coarse, and perhaps relatively slow, modulation of information transmission in the principal pathways connecting V1 and V2 to the parietal and temporal lobes*. A better appreciation of the role of V3/VP might have to await studies that explore the effects of damage confined to it.

5.3 MT (V5)

MT is firmly implicated in the analysis of movement. Cells there have distinctive receptive fields, showing pronounced selectivity for direction of movement, often without much selectivity for other attributes of the stimulus (Zeki 1974; Van Essen et al 1981; Albright 1984; Movshon et al 1985). Within the fine-structure of the retinotopic map neurons seem to be clustered by direction preference (Albright et al 1984). Newsome et al (1985) showed that damage to MT impairs a monkey's capacity to pursue moving stimuli, and Newsome and Paré (1988) showed that damage to MT impairs for a time a monkey's capacity to report the direction of motion of a noisy field of moving dots, but leaves contrast sensitivity unimpaired; Andersen and Siegel (1990) found that monkeys temporarily lost their capacity to detect structured movement in dynamic dots displays. Salzman et al (1992) later showed that electrical stimulation confined to a cluster of MT cells that prefer the same direction of motion biases monkeys' reports about direction of movement. These observations tie MT to the perception of movement, but movement of what? The relative indifference of cells to the spatial attributes of the stimulus implies some abstract analysis of movement that is easily accommodated by either of the contrasting views of cortical organization that I have been discussing. On one view,

the signals from MT are at some later stage reconciled with information about other image attributes, giving rise to the coherent perception of moving objects. On the alternative view, which I prefer, the separation of motion signals from signals about other dimensions of image variation means that the analysis they subservise is self-contained.

Two tasks in which MT has been implicated—the control of pursuit eye movements and the analysis of optic flow—seem to fit this requirement nicely. Neither task requires much information about the structure of objects,⁽⁸⁾ and neurons in MT seem to be usefully ignorant of structure. But more than that, movement through the normal visual environment produces a pattern of optic flow that is much richer in the lower visual field, and this is curiously well-matched to the retinotopy of MT, which disproportionately represents a sector of the lower temporal visual field radiating obliquely from the fovea (Maunsell and Van Essen 1987). Moreover, in the more peripheral parts of the visual field the preferred direction of motion in receptive fields tends to radiate away from the fovea (Albright 1989). These facts alone make no convincing case that MT is important for the analysis of optic flow, but the argument is considerably strengthened by the observation that MT provides the major input to the middle superior temporal area (MST) (Maunsell and Van Essen 1983; Boussaoud et al 1990), where cells do seem to be well equipped for the analysis of optic flow (Duffy and Wurtz 1991, 1995). My point here is not that MT contributes little to the conscious perception of movement—it evidently does—but that its contribution might have little to do with the segmentation of *surfaces* by movement or with articulating the movements of *objects*. Although Stoner and Albright (1992) have shown that some MT neurons respond differently to plaid patterns that (to a human observer) appear to move coherently and those that appear to slide, before accepting that MT cells contribute to the discovery of surface structure one would want to know that no cells in other areas do the job better.

5.4 V4

V4 draws its principal input from V2 (Felleman and Van Essen 1983). Although V4 is half the size of V2, no visual area beyond it is nearly as big, so we might expect it to contribute something substantial to the analysis of the image. The first physiological exploration (Zeki 1973) drew attention to the color-selectivity of cells. Later work has emphasized this less, pointing out that the chromatic characteristics of cells in V4 are much like those of cells in V1 (Krüger and Gouras 1980; Schein et al 1982), and has stressed that the fundamental selectivities of V4 cells to orientation, spatial frequency, and direction of movement are in most respects like those of cells in V1 (Desimone and Schein 1987). We know little about how different dimensions of stimulus analysis are represented in V4. Zeki (1973) found cells clustered in columns by chromatic preference; no other grouping principle has been observed, though functional clustering must be suspected from the selectivity of tracer uptake in different kinds of V2 stripes after a localized V4 injection (Van Essen et al 1990), and from the patchy projection it receives from V3. V4 cells can be difficult to drive, and more of them than in V2 or V1 seem to be visually unresponsive (Krüger and Gouras 1980; Schein et al 1982). This makes one suspect that the optimal stimuli might be more complex than those commonly used to explore receptive fields. One example of this is Desimone and Schein's (1987) finding of complex cells that respond selectively to gratings of high spatial frequency, but in any orientation. Other examples are provided by Gallant et al (1993), who show that radial or spiral patterns are for some cells more effective stimuli than any simpler grating patterns.

Many neurons in V4 share with V2 the property of having relatively fine spatial selectivity (eg, for spatial frequency and orientation) within a large receptive field (Desimone and Schein 1987). As in V2, receptive fields overlap each other more than

⁽⁸⁾ Koenderink (1986) reviews the information available in optic flow.

in other occipital areas, and offer potentially rich opportunities for spatial integration. No one has explored how cells integrate signals from disjointed stimuli that fall in the receptive field, but Desimone and Schein's (1987) results suggest that their responses might be complicated, for, when stimulated by a single bar, some cells respond only if the bar is much shorter than the region within which it can be placed to excite a response. It would be most valuable to know whether this represents a genuine indifference to the spatial position of the preferred stimulus, or indicates that the preferred stimulus is not the bar but some complex aggregate of which the bar is a part. Why might we expect the latter?

Nothing we learned about V2 suggests that it does more than establish continuity of structure locally (albeit in a cyclopean image), so important problems remain to be solved in finding surfaces. Two obvious ones are to discover higher-order aspects of surface structure—eg, patterns that repeat on a larger scale, gradients of texture and brightness—that will allow discovery of discontinuities, and to attribute a discontinuity in structure to only one of the regions that create it. The latter is the problem of figure-ground segregation, made so conspicuous by ambiguous figures, but always present and apparently solved effortlessly most of the time. Perceptual work suggests that among the factors that determine figure-ground organization are surroundedness, symmetry, convexity, orientation, and color or lightness contrast (Rock 1986). The processes involved are apparently cooperative (Attneave 1971), and ensure that only a single interpretation is available at any moment. Might V4 be especially equipped to discover some of these structural relations? It is not obvious that it could help us with all of them (for example, most biologically significant symmetry is about the vertical mid-line), but what little we understand of receptive field organization suggests it is rich enough to accommodate elaborate analysis of various kinds of gradients in image structure.

Zeki (1983a, 1983b) first observed that the response of a cell in V4 to a colored patch depends substantially on the color of light falling on surrounding regions, being generally more vigorous when the surrounding light has a different spectral composition—indeed the effect seems to be so strong that some cells cannot be driven in the absence of the color contrast (Zeki 1983b). The mechanism involved seems to have two components: illumination of the surround suppresses the response to the preferred stimulus when the light is the same color, and may also increase the response to the preferred stimulus when it is of near-complementary color (Schein and Desimone 1990). Zeki pointed out that by weakening responses to large regions of common chromaticity the contrast phenomena might promote the constancy of color appearance in the face of changing illumination, but I think it means something different, and is an expression of a more general characteristic that makes the cell sensitive to contrast in image structure.⁽⁹⁾ Desimone and Schein (1987) showed that for many cells the large, silent region is not isotropic: silent inhibition flanking the excitatory region might be accompanied by silent facilitation at its ends. Moreover, Desimone et al (1985) observed that the surround inhibition is not just color-specific: whatever the stimulus preferred by the excitatory region of the receptive field, that was often the most effective suppressor stimulus when placed in the silent region. The latter observation was confirmed by Müller et al (1996) who also showed that when the excitable field was filled with a grating of the preferred orientation, and the surrounding region with a grating of a contrasting orientation, a cell could respond more vigorously than when only the excitable region is stimulated.

⁽⁹⁾One attractive feature of Zeki's proposal is that the large receptive fields in V4 provide a mechanism for substantial spatial integration of signals—an important requirement for color constancy. However, an equivalent integration could be achieved by spatially localized mechanisms that have long time-constants of adaptation, and which through eye movements are exposed to varied parts of a scene. Neurons in LGN appear to have some of the required properties (DePriest et al 1991).

Schein and Desimone (1990) suggested that the contrast mechanism might establish figure–ground segregation. It seems to me unlikely that V4 solves the whole problem, for figure–ground segregation requires not only the articulation of surfaces but their attribution to object and background, and I think it may be unwise to conceive of the ‘figure’ as whatever falls in the excitatory part of the receptive field. Rather, it might be productive to think of a V4 cell as a ‘detector of structural contrast’ that finds gradients or discontinuities in structure, by analogy with the way that a ganglion cell finds a gradient in luminance. A region of uniform structure does not excite a V4 cell well, but a gradient of structure does. As a result, V4 might articulate regions and prevent the simultaneous assignment of a single region to two surfaces. Not much physiological evidence bears on this suggestion. We would like to know how general is the capacity to detect contrast: for example, along which dimensions (beyond color and orientation) can a cell detect contrast? (Most especially, in view of the demonstrated sensitivity of MT neurons to moving patterns, how does a V4 cell respond to stimuli defined by motion contrast?) Within a given dimension, is a cell sensitive to a contrast between two particular points on the dimension, or to any two points separated by a certain distance? Is there any cooperative interaction when the stimuli on the excitable receptive field and the surrounding region differ along multiple dimensions? How does a cell behave when the contrasts on different dimensions are out of phase?

Although single-unit recording provides only uncertain pointers to the work done by V4, a role in the analysis of configuration is also indicated by the effects of experimental lesions. Damage confined to V4 only modestly impairs monkeys’ performance on a variety of simple detection and discrimination tasks, with no dimension of stimulus variation being particularly vulnerable (Heywood and Cowey 1987; Heywood et al 1992; Merigan 1996), but severely disrupts performance on tasks that require monkeys to distinguish the forms (Heywood et al 1992; Merigan 1996; De Weerd et al 1996) or the sizes (Schiller 1993) of objects.

5.5 *Summary and assessment*

The account of visual organization I have developed here is at odds with the notion that different attributes of the image are analyzed in multiple pathways. Rather, I have suggested that within occipital cortex one pathway, with an emphasis on the peripheral visual field, makes a fairly abstract analysis of movement to uncover information about optic flow; while another pathway, with an emphasis on the central visual field, analyzes all the dimensions of the image, including movement, related to object vision. On this conception the results of the two analyses need never be brought together (or if they are, only tenuously), because they support quite distinct kinds of perceptions and behaviors; all the dimensions of analysis relevant to object vision are everywhere tightly coupled.

The modularity of analysis embodied in this scheme appears principally in the vertical organization of the system and, although not of the sort commonly thought to be most beneficial, has interesting implications. The argument has been that at each level in the hierarchy the machinery is capable of making decisions about image properties of a certain complexity.

Figure 7 summarizes what might be accomplished at different levels. Striate cortex seems well-equipped to make decisions about many of the thresholds we commonly measure (eg, contrast sensitivity—both achromatic and chromatic—acuity, flicker, spatial frequency discrimination, orientation discrimination); V2 finds continuity in the local structure of the image and decides what to do with the possibly disparate images from the two eyes, fusing them or ultimately suppressing one as appropriate; V4 discovers surface structure on a larger scale, tagging discontinuities in structure as belonging to only one of the regions that provide their definition, and forbidding the simultaneous

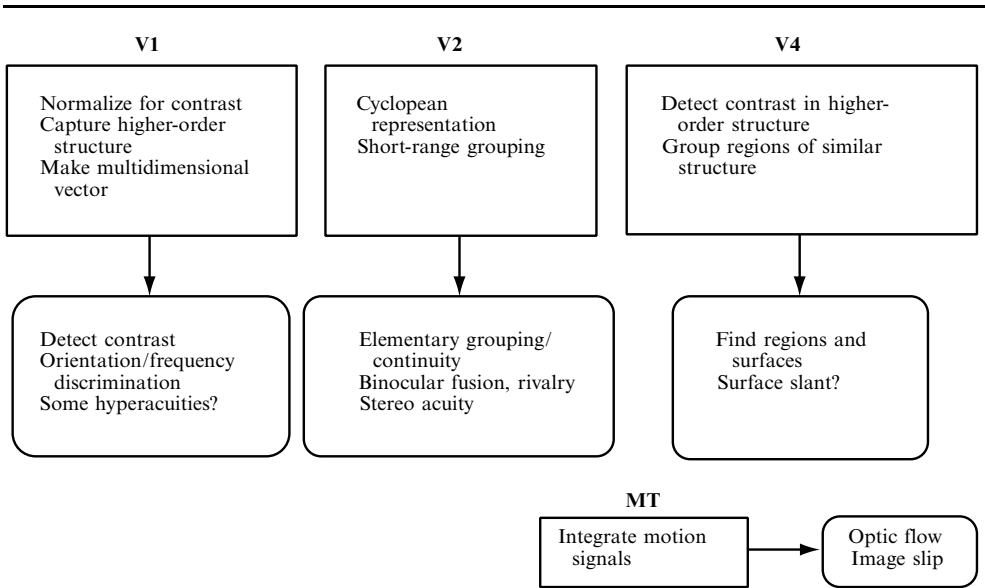


Figure 7. Summary of the kinds of perceptual decisions that might be made by visual areas at different levels in the cortical hierarchy. For each area the upper box indicates operations undertaken; the lower box indicates perceptual roles.

assignment of a single region to two surfaces. The important corollary idea is that each level passes on to the one above only the *results* of its analysis, so that, for example, the local continuity that V2 finds is expressed to V4 as continuous structure of a certain class, but V4 knows nothing about the information used to discover that structure, and cannot be interrogated about the detail of it. Presumably higher levels in the system continue in the same way. This suggestion is entirely consistent with the non-linear behavior of most cortical cells, which results in them discarding a great deal of information: one could not reconstruct the visual stimulus that excited a cell from an analysis of its responses. It also explains why areas become smaller as one rises in the visual cortical hierarchy: cumulatively larger numbers of decisions about the image have been made at lower levels. The idea that each area passes on *decisions* about image structure at a particular level of analysis means not only that V4 is ignorant of the information used by V2, but that in some sense V4's interpretation of the image will be an alternative to the one produced by V2. This principle readily accommodates the otherwise difficult notion that, perceptually, we always have concurrent access to different levels of description of the image.

The scheme I have argued for has two important features in common with Marr's (1982)—the hierarchical nature of the analysis, and the accessibility to consciousness of the analysis undertaken at each level—but it differs sharply in its emphasis on modularity and parallelism, which here is implicit in the multidimensionality of analysis, and is explicit only in a motion pathway that I have argued is quite special. There are interesting parallels and important differences between the stages of analysis here associated with different visual areas and the stages articulated by Marr. Marr's lowest-level entity—the primal sketch—is in some respects as rich a representation of the image as anything discussed here. The processes that form the *raw primal sketch* encompass all that here is attributed to V1 (finding primitives on multiple dimensions on multiple scales) and much of what is here attributed to V2 (finding continuity in local structure). The elaboration of the raw primal sketch into the *full primal sketch* depends on grouping processes that would here be the job of V4. The stage beyond, the $2\frac{1}{2}$ -D sketch, makes explicit the three-dimensional structure of surfaces, but does

not represent, for example, information about the angles between surfaces. In the present account, the local three-dimensional structure given by analysis of disparities is explicit earlier, in V2, while other information about surface orientation, such as texture gradients, shading, and occlusions, could not be discovered until V4.

6 Some objections

6.1 *Separability of perceptual components*

One thing that might be thought missing from this account is that it does not explain some of the more persuasive perceptual evidence for independent analysis of different attributes of the image. In visual search tasks, the immediacy with which a target sometimes ‘pops out’ of distractors has been taken as evidence that fundamental target attributes (eg, colors, orientations, sizes) are analyzed independently: a target will pop out from distractors when it, but not distractors, possesses a critical attribute; a target defined by a conjunction of attributes will pop out only if none of its attributes are shared by distractors (Treisman 1988). In early work (Treisman and Gelade 1980) it seemed that a few attributes were fundamental, in the sense of permitting pop-out, but recent work has demonstrated pop-out of targets defined by conjunctions of many kinds of stimulus differences (Nakayama and Silverman 1986; Wolfe et al 1989; D’Zmura 1991), and it now seems more appropriate to regard pop-out as a reflection of the discriminability of the target and distractors (Palmer 1994; Verghese and Nakayama 1994).

Perhaps the most impressive evidence for modular analysis in vision comes from studies of specific perceptual impairments that result from damage to cortex. In the present context the most interesting are those where a deficit is confined to a visual submodality. Only movement perception and color perception have received attention, and disturbances of the former are exceptionally rare (Grüsser and Landis 1991). A dissociation of movement perception and object perception is not necessarily troublesome for the argument made here, which recognizes a special pathway for analysis of some aspects of movement. The interesting question is whether the clinical evidence supports a distinction between an analysis that deals with self-motion and an analysis that contributes to the recovery of surfaces and object structure. There is not enough evidence to decide: in the most thoroughly studied case (Zihl et al 1983; Hess et al 1989; Baker et al 1991), the subject had extensive bilateral occipito-temporal lesions that disturbed not only motion perception, but also reading and drawing (Grüsser and Landis 1991).

Specific disturbances of color vision are potentially more troublesome, for nowhere in the scheme I have outlined is there any provision for a color module. There are two issues to consider: evidence on the selectivity of deficit, and evidence on the level of deficit. Most cases of acquired achromatopsia are accompanied by visual deficits of other kinds in the same region of the visual field; some of the most specific have resulted from damage to the lingual and fusiform gyri (Zeki 1990). For our purposes the question about these is not so much *is the loss specific*, but *is what has been lost the capacity to use color differences to reveal structure in images?* If what is lost is the capacity to *identify* colors and to name the colors of surfaces and objects, without commensurate impairment of the capacity to articulate and *distinguish* surfaces that are differently colored, the deficiency can be thought of as a high-level one that involves visual memory, and could well lie at a stage—beyond any discussed here—where information about color is abstracted from the multidimensional image description. Little work bears on the issue. The painter described by Sacks et al (1988), who saw no color following a blow to the head, could distinguish though not identify image components of different colors; he could conjure up only achromatic visual images. The subject studied by Victor et al (1989) could discriminate hues and use color to segment surfaces, but had great difficulty naming colors of unfamiliar objects and forming groups of items of similar color. Mollon et al (1980) and Barbur et al (1994) describe apparently similar

cases. It seems to me that these kinds of defects reflect an impaired capacity to make sense of color differences—to know what they signify—and implicate higher-level mechanisms than I believe are contained in V4. Moreover, the size of V4 (it is substantially the largest area beyond V2) and its anatomical position (it is the gateway to the temporal lobe) necessitate that it do more than just support color vision.

Recent analyses of local changes in cerebral blood flow brought about by viewing colored stimuli point to there being a cortical region specifically sensitive to color (Corbetta et al 1991; Zeki et al 1991). The evidence for a 'hot spot' is persuasive, but it is not entirely clear that the chromatic characteristics of the visual stimulus are what light up the hot spot. For example, in the study by Zeki et al (1991) the contrasting stimuli were a colored 'Mondrian' pattern and the same pattern with the colored patches replaced by grays of the same luminances. There seems little doubt that the former pattern is much more salient (the structure of the latter could, in principle, have been invisible); a more interesting control pattern might have been one comprised of patches defined by different textures.

Overall, I believe the evidence is against particular cortical areas being specialized for the analysis of a single attribute of the image.

6.2 *Richness of interconnections*

In describing the connections among cortical areas I have ignored many of them, both among visual areas and between visual areas and non-visual ones. In the case of V4, for example, Tanaka et al (1990) estimate that only 35% of the input comes from V2 and V3/VP. My most egregious omission has to do with reciprocity: in almost every case where there is a forward projection from one area to another, there is a projection in the opposite direction, often maintaining retinotopy (Felleman and Van Essen 1991). The key issue is whether these feedback connections couple areas in ways that *dynamically* shape the analysis, or provide a signal that less immediately controls it. If the former, then it makes little sense to formulate, as I have done, a scheme that treats each area as a unit capable of relatively independent action.

Feedback is crucial in models of object recognition that rely on analysis by synthesis (eg Mumford 1994). Here recognition proceeds by iteration, with higher levels in the system generating a guess about the meaning of the incoming signal, and feeding this back to lower levels to generate what is in essence a synthetic image that can be compared with the image delivered from the retina.

The most persuasive argument against this kind of scheme is that neurons in the higher reaches of the visual system deliver stable responses too quickly, and visual reaction times are too fast, for the analysis to be moderated by feedback (Thorpe and Imbert 1989). Neurons in inferotemporal cortex respond with latencies of ca 125 ms to effective stimuli (Oram and Perrett 1992) and the early few tens of milliseconds of a response contain most of the information transmitted by a neuron (Tovée et al 1993). These latencies do not much exceed the latencies of responses recorded in V1 and V2 (ca 70–100 ms: Celebrini et al 1993; Nowak et al 1995);⁽¹⁰⁾ moreover, the selectivities of neurons in V1 are fully developed and stable within 10–20 ms of response onset (Celebrini et al 1993), making it very unlikely that feedback from higher areas shapes the visual characteristics of neurons. It seems more likely that feedback from higher areas is distantly involved in controlling the behavior of neurons. Other evidence, from the recordings in LGN, where the effects of feedback have been explored thoroughly, points to the same conclusion. A huge number of fibers run from striate cortex to LGN (Lund et al 1975), making perhaps more synaptic connections than the incoming fibers

⁽¹⁰⁾ Synaptic delays measured after electrical stimulation are often as short as 1–2 ms, but much longer delays, reflecting integration of EPSPs, are likely following visual stimulation (Maunsell and Gibson 1992).

from the retina (Robson 1983). In cat, feedback has modest effects on the selectivities of neurons (eg Murphy and Sillito 1987; Gulys et al 1990); in monkey it appears to have no consistent effect on the receptive field properties of neurons, instead bringing about changes in responsiveness (Marrocco et al 1982; McClurkin et al 1994).

Several modulating functions, some general and some quite specific, might be served by feedback connections. First, the visual system might need to regulate the gain of transmission between areas: the increase in receptive field size from one level to the next brings with it the difficulty of ensuring that a cell with a limited dynamic range is adequately sensitive to small stimuli but not too readily saturated by large ones. Sclar et al (1990) explored spatial summation in the large receptive fields of cells in MT and concluded that some gain-controlling mechanism must be involved in regulating their sensitivities. Feedback connections are attractive candidates for this. Second, feedback might provide the means whereby focal attention changes the excitability of neurons in defined regions of the visual field. Such effects are seen in V1 and higher areas (Moran and Desimone 1985; Motter 1993; Treue and Maunsell 1996), particularly when several potential targets are present in the visual field. The decision to direct attention probably originates at a high level, and for selection by location rather than by visual content is presumably most efficiently exercised at a low level in the pathway.⁽¹¹⁾ Attentional selection for image content must depend on analyses that articulate visual features or objects, so, if different visual areas articulate features of different complexity, feedback at different levels could control sensitivity to features of appropriate complexity. Neurons in V4 are clearly susceptible to this kind of attentional regulation (Motter 1994a, 1994b); those in V1 are less so (Haenny and Schiller 1988). Third, feedback connections might activate lower areas during visual imagery. Whether or not lower areas are activated is controversial (Roland and Gulys 1994; Kosslyn et al 1995), but were they to be (implying considerable specificity of feedback), an area activated by feedback presumably would send signals to all the places it does during visual activation. A related notion, suggested to me by N Graham, is that feedback might help sustain (as short-term memory) the description of an image just seen. Fourth, feedback might control the level at which the visual system delivers a description of an image. I have argued that each level in the hierarchy provides a description of the image at a different level of aggregation, with the detail available at one level being inaccessible at the level above. In a real sense then the visual system generates competing descriptions of the image. We appear to entertain these concurrently (we can see both a face and the freckles), but that seems to be an illusion that belies our capacity to switch attention from one level to another.⁽¹²⁾ To ensure that at any instant we have a unique interpretation of the image we engage attention to select one description while inhibiting others; descending connections might provide a ready means for biasing the selection in favor of a particular level of description (ensuring, for example, that we are predisposed to see a rough surface rather than the textural detail of its makeup). Fifth, feedback might be used to set the confidence level at which decisions are made in different visual areas. For example, in the context of a psychophysical discrimination that depends upon V1, feedback might be used to set the criterion that results in a decision for or against a particular visual stimulus.

Yet other, and more distant, roles for feedback connections are suggested by computational work aimed at understanding how we classify visual objects. Many classifiers use backpropagation to adjust the weights of signals in neural networks. This makes explicit

⁽¹¹⁾ The LGN, rich in feedback connections and a compact bottleneck in the transmission of visual information, ought to be the optimal place for attentional regulation of visual sensitivity by location in the visual field. No work seems to have been done to explore this.

⁽¹²⁾ Mary Hayhoe pointed out to me the potential importance of attention in suppressing competing interpretations of the image.

the need for feedback connections, but these are used only while the network is being trained, not to sustain the normal function of the classifier, and (beyond the interesting implication that learning occurs at low levels in the visual pathway) have little bearing on the arguments developed here. Although feedback signals are iteratively involved in some models of self-supervised learning (eg Hinton et al 1995), the feedback does not directly influence the normal forward operation of the classifier.

6.3 *Access to consciousness*

I have argued that all levels of the visual cortical hierarchy make perceptual decisions. This idea might be challenged on the ground that visual awareness, and by implication the capacity to make perceptual decisions, requires the integrity of higher visual areas (Crick and Koch 1995). Reliable perceptual decisions need not depend on conscious awareness, but it is nonetheless reasonable to ask if lower areas can provide the capabilities I have suggested. We might look first for evidence that each visual area has efferent pathways (capable of conveying perceptual decisions) that bypass immediately higher areas in occipital cortex, and evidence that disruption of these pathways results in failure to perceive the low-level elements of visual structures, without concomitantly impaired perception of the surfaces and objects formed from aggregates. There is little anatomical evidence on such pathways, but Marshall and Halligan (1995) described a woman who, following an infarction that damaged frontal and parietal cortex, was able to perceive forms composed of aggregates of elementary forms, but could not perceive the elementary forms. This is the sort of behavior one might expect to result from disruption of efferent pathways originating at lower levels in the visual system.

We can also ask the complementary question: what visual functions remain when only these putative efferent pathways survive—when higher centers are damaged? Here the evidence from monkey is clear: damage to V2, for example, leaves monkeys well able to make discriminations of luminance, color, and orientation (Merigan et al 1993); damage to V4 causes only mild impairments of performance on a range of simple discriminations, but severely disrupts shape discrimination (Merigan 1996). Some people with probable V2 lesions report that they cannot see (Horton and Hoyt 1991); this is to be contrasted with many clear cases in whom damage is bilateral, primarily to occipital cortex beyond V1, and who suffer from ‘apperceptive agnosia’. Apperceptive agnosics have normal or nearly normal visual fields, increment sensitivity, movement thresholds, color discrimination, etc; they can distinguish textures, and can perceive contour locally and see limited connectedness of visual elements, but cannot trace across a break in a line and are quite unable to make elementary distinctions about the shapes of surfaces (Farah 1990). They are often considered blind.

6.4 *So little has been achieved*

Perhaps the most troublesome objection to the picture I have developed is that an enormous amount of cortex is used to achieve remarkably little. Nearly 60% of known visual cortex lies in the areas I have discussed, yet all that has been achieved is to articulate surfaces and their positions. Is it reasonable to suppose that all the rest of vision—the recognition of objects and their placement in an object-centered space rather than a retinotopic space—could be accomplished by so little machinery? I think the answer must be yes, and that we are uneasy about it because the generally complete comprehensibility of our visual world induces us to misrepresent the problem. There are two sides to this: we underestimate the importance of what is achieved by recovering surface structure, and we overestimate the work that remains to be done.

A useful way to remind ourselves of the importance of the earlier stages is to consider the capabilities of people in whom they might have been damaged. Apperceptive agnosics (above), whose perceptual deficit is closely tied to damage in occipital cortex beyond V1, are close to being functionally blind (Farah 1990). Contrast these people with others

(associative agnosics and optic aphasics) whose disability is often associated with damage to occipito-temporal cortex, and which lies not in their capacity to articulate the structure of a scene (inferred from their relatively unimpaired capacity to draw objects or recognize when objects are the same), but in their capacity to identify (visual) objects by naming them or demonstrating their use. Although their commerce with the world is often difficult, these people clearly have access to a lot of visually derived knowledge about its structure (Farah 1990). This caricature of the apperceptive and associative agnosias captures much of the distinction I am trying to draw between what might have been done in occipital cortex, and what is left for the rest of the system to do. How difficult is the latter stage?

The problem of recognition is to match a description currently in hand to one stored. There is no doubt about the richness of detail in the description at hand, but how much detail is in the stored description? Marr (1982) argued that visual recognition required comparison of three-dimensional descriptions in an object-centered space, and these are demonstrably hard to construct. However, the visual system may not need anything so elaborate in recognizing objects, instead solving the problem through manipulation of two-dimensional images (Ullman 1992; Logothetis et al 1994). Whatever is stored ought to contain as little information as is needed for reliable performance; I believe that the stored description might be quite rudimentary and that we can get some idea of what it contains by considering the quality of our visual imagery. That is, we treat the mental image as the result of non-visual activation of the stored representation; the detail available in the mental image reflects that precision of the memory.

There is good reason to believe that visual imagery depends on cortex in the occipito-temporal region, which both scalp recordings of event-related potentials (Farah et al 1989) and studies of cerebral blood flow (Roland and Friberg 1985; Goldenberg et al 1987) show to be especially active while a subject imagines a visual object. Moreover, people who have suffered brain damage that impairs their vision often lose the capacity to visualize (Farah 1988);⁽¹³⁾ the case of Sacks et al (1988) is an example. Consider now the image we can conjure up when asked to imagine a spouse or offspring. For most of us it will be a remarkably impoverished representation—one from which many of us could not extract much detail, and in which the resolution is poor (Finke and Kosslyn 1980)—yet it regularly supports precise and reliable decisions about the familiar and unfamiliar objects in real visual images. My point is that relatively little information needs to be stored to distinguish the visual objects we normally deal with, so the richness of our visual world derives mostly from what is immediately experienced, and is volatile and built anew with each inspection. Another illustration of the same point is the contrast between the apparent clarity of our peripheral vision and the lack of detail we discover from careful scrutiny of it: we are generally unaware of this because the relatively impoverished information delivered by the periphery is often sufficient for recognition, and can be enriched on demand by moving the eyes. Our dependence on the analysis that precedes recognition is what justifies the enormous investment in machinery at that level.

7 Concluding remarks

In discussing V1 I took the position that a single unit represents a value on a multi-dimensional vector that describes the image locally. Despite units being relatively coarsely tuned on each dimension, few will match on all dimensions the local structure of an image. We know too little to estimate the number of V1 neurons that normally contribute to perceptual decisions, but, given the likelihood that their properties are

⁽¹³⁾This is a tremendously important observation, for it explains why it is so difficult to learn from cases of brain damage what the visual work of the patient is like. Without the capacity for visual imagery it becomes exceptionally hard to express visual experience in a form that can be communicated to others.

well-matched to the statistics of natural scenes (Field 1994), and how few are needed for spatial localization (Parker and Hawken 1985), I think the number must be small. In V2 the receptive fields of neurons are larger and are postulated to be sensitive to continuity in local structure, so relatively fewer will be driven by natural images; by extension, the same will be more true of V4, which we suppose discovers more complex structure. The hierarchy can be seen as a mechanism for producing a progressively sparser description of the image, by dealing with it in more complex aggregates.

Granted that activity in a single neuron is perceptually significant, can we discern the significance with single-unit recording? The major weakness of single-unit recording as an instrument of discovery is not so much that we miss the overall characteristics of a visual neuron—I think that these are probably captured relatively well in most experiments—but that precisely because the gross properties are often easily discerned we are more likely to overlook key characteristics that are subtly expressed, for example details of spatial integration, or binocular summation. A different kind of problem, and one that is probably more troublesome, results from the way we describe the measurements we make. We can convey many important properties of a simple cell by calling it a bar detector, but we are likely to be misled if we infer from that neat summary that the job of a simple cell is to detect bars. Single-unit recording on its own is a weak instrument for discovering what cortex really does, but when harnessed to a theory it is immensely valuable.

Acknowledgements. This work was supported by the National Eye Institute through grants EY 04440 and EY 01319. In refining the arguments developed here I have benefitted greatly from the comments of Horace Barlow, Andrew Derrington, Norma Graham, Robert Jacobs, Jonathan Levitt, John Maunsell, Suzanne McKee, Andrew Metha, Tony Movshon, Jim Müller, and Andrew Parker.

References

- Adelson E H, Bergen J R, 1991 “The plenoptic function and the elements of early vision”, in *Computational Models of Visual Processing* Eds M S Landy, J A Movshon (Cambridge, MA: MIT Press) pp 1–20
- Albers R W, Siegel G J, Stahl W L, 1994 “Membrane transport”, in *Basic Neurochemistry* Eds G J Siegel, B W Agranoff, R W Albers, P B Molinoff (New York: Raven) pp 49–73
- Albrecht D G, Geisler W S, 1991 “Motion selectivity and the contrast-response function of simple cells in the visual cortex” *Visual Neuroscience* **7** 531–546
- Albright T D, 1984 “Direction and orientation selectivity of neurons in visual area MT of the macaque” *Journal of Neurophysiology* **52** 1106–1130
- Albright T D, 1989 “Centrifugal directional bias in the middle temporal visual area (MT) of the macaque” *Visual Neuroscience* **2** 177–188
- Albright T D, Desimone R, 1987 “Local precision of visuotopic organization in the middle temporal area (MT) of the macaque” *Experimental Brain Research* **65** 582–592
- Albright T D, Desimone R, Gross C G, 1984 “Columnar organization of directionally selective cells in visual area MT of the macaque” *Journal of Neurophysiology* **51** 16–31
- Andersen R A, Siegel R M, 1990 “Motion processing in the primate cortex”, in *Signal and Sense: Local and Global Order in Perceptual Maps* Eds G M Edelman, W E Gall, W M Cowan (New York: John Wiley) pp 163–184
- Atick J J, 1992 “Could information theory provide an ecological theory of sensory processing?” *Network* **3** 213–251
- Attneave F, 1954 “Informational aspects of visual perception” *Psychological Review* **61** 183–193
- Attneave F, 1971 “Multistability in perception” *Scientific American* **225** (December) 62–71
- Baddeley R, 1996 “An efficient code in V1?” *Nature (London)* **381** 560–561
- Baddeley R J, Hancock P J B, 1991 “A statistical analysis of natural images matches psychophysically derived orientation tuning curves” *Proceedings of the Royal Society of London B* **246** 219–223
- Baizer J, 1982 “Receptive field properties of V3 neurons in monkey” *Investigative Ophthalmology & Visual Science* **23** 78–95
- Baizer J S, Robinson D L, Dow B M, 1977 “Visual responses of area 18 neurons in awake, behaving monkeys” *Journal of Neurophysiology* **40** 1024–1037

- Baker C L Jr, Hess R F, Zihl J, 1991 "Residual motion perception in a 'motion-blind' patient, assessed with limited-lifetime random dot stimuli" *Journal of Neuroscience* **11** 454–461
- Ballard D H, 1986 "Cortical connections and parallel processing: structure and function" *The Behavioral and Brain Sciences* **9** 67–120
- Barbur J L, Harlow A J, Plant G T, 1994 "Insights into the different exploits of colour in the visual cortex" *Proceedings of the Royal Society of London B* **258** 327–334
- Barlow H B, 1953 "Summation and inhibition in the frog's retina" *Journal of Physiology (London)* **119** 69–88
- Barlow H B, 1960 "The coding of sensory messages", in *Current Problems in Animal Behaviour* Eds W H Thorpe, O L Zangwill (Cambridge: Cambridge University Press) pp 331–360
- Barlow H B, 1972 "Single units and sensation: a neuron doctrine for perceptual psychology?" *Perception* **1** 371–394
- Barlow H B, 1981 "The Ferrier lecture. Critical limiting factors in the design of the eye and visual cortex" *Proceedings of the Royal Society of London B* **212** 1–34
- Barlow H B, 1985 "The twelfth Bartlett memorial lecture: the role of single neurons in the psychology of perception" *Journal of Experimental Psychology* **37A** 121–145
- Barlow H B, 1986 "Why have multiple cortical areas?" *Vision Research* **26** 81–90
- Barlow H B, Blakemore C, Pettigrew J D, 1967 "The neural mechanisms of binocular depth discrimination" *Journal of Physiology (London)* **193** 327–342
- Barlow H B, Hill R M, Levick W R, 1964 "Retinal ganglion cells responding selectively to direction and speed of image motion in the rabbit" *Journal of Physiology (London)* **173** 377–407
- Barrow H G, Tenenbaum J M, 1978 "Recovering intrinsic scene characteristics from images", in *Computer Vision Systems* Eds A R Hanson, E M Riseman (New York: Academic Press) pp 3–26
- Barrow H G, Tenenbaum J M, 1986 "Computational approaches to vision", in *Handbook of Perception and Human Performance* Eds K R Boff, L R Kaufman, J P Thomas (New York: John Wiley) pp 38:1–38:70
- Bauman L A, Bonds A B, 1991 "Inhibitory refinement of spatial frequency selectivity in single cells of the cat striate cortex" *Vision Research* **31** 933–944
- Bergen J R, Adelson E H, 1988 "Early vision and texture perception" *Nature (London)* **333** 363–364
- Bergen J R, Landy M S, 1991 "Computational modeling of visual texture segregation", in *Computational Models of Visual Processing* Eds M S Landy, J A Movshon (Cambridge, MA: MIT Press) pp 253–271
- Biederman I, 1987 "Recognition-by-components: a theory of human image understanding" *Psychological Review* **94** 115–147
- Blake R, 1989 "A neural theory of binocular rivalry" *Psychological Review* **93** 145–167
- Blakemore C, Tobin E A, 1972 "Lateral inhibition between orientation detectors in the cat's visual cortex" *Experimental Brain Research* **15** 439–440
- Blasdel G, 1992 "Orientation selectivity, preference, and continuity in monkey striate cortex" *Journal of Neuroscience* **12** 3139–3161
- Bonds A B, 1989 "Role of inhibition in the specification of orientation-selectivity of cells in the cat striate cortex" *Visual Neuroscience* **2** 41–55
- Bonds A B, 1991 "Temporal dynamics of contrast gain in single cells of the cat striate cortex" *Visual Neuroscience* **6** 239–255
- Bonhoeffer T, Grinvald A, 1991 "Iso-orientation domains in cat visual cortex are arranged in pinwheel-like patterns" *Nature (London)* **353** 429–431
- Born R T, Tootell R B H, 1991 "Spatial frequency tuning of single units in macaque supragranular striate cortex" *Proceedings of the National Academy of Sciences of the USA* **88** 7066–7070
- Bossomaier T, Snyder A W, 1986 "Why spatial frequency processing in the visual cortex?" *Vision Research* **26** 1307–1309
- Boussaoud D, Ungerleider L C, Desimone R, 1990 "Pathways for motion analysis: cortical connections of the medial superior temporal and fundus of the superior temporal visual areas in the macaque" *Journal of Comparative Neurology* **296** 462–495
- Braddick O J, 1979 "Binocular single vision and perceptual processing" *Proceedings of the Royal Society of London B* **204** 503–512
- Bradley A, Switkes E, De Valois K, 1988 "Orientation and spatial frequency selectivity of adaptation to colour and luminance gratings" *Vision Research* **28** 841–856
- Buchsbaum G, Gottschalk A, 1983 "Trichromacy, opponent colours coding and optimum colour information transmission in the retina" *Proceedings of the Royal Society of London B* **220** 89–113

- Burkhalter A, Felleman D J, Newsome W T, Van Essen D C, 1986 "Anatomical and physiological asymmetries related to visual areas V3 and VP in macaque extrastriate cortex" *Vision Research* **26** 63–80
- Burkhalter A, Van Essen D C, 1986 "Processing of color, form, and disparity information in visual areas VP and V2 of ventral extrastriate cortex in the macaque monkey" *Journal of Neuroscience* **6** 2327–2351
- Burton G J, Moorhead I R, 1987 "Color and spatial structure in natural scenes" *Applied Optics* **26** 157–170
- Cavanagh P, 1989 "Multiple analyses of orientation in the visual system", in *Neural Mechanisms of Visual Perception* Eds D M-K Lam, C Gilbert (Woodlands, TX: Portfolio Publishing) pp 261–280
- Celebrini S, Thorpe S, Trotter Y, Imbert M, 1993 "Dynamics of orientation coding in area V1 of the awake primate" *Visual Neuroscience* **10** 811–825
- Churchland P S, Sejnowski T J, 1992 *The Computational Brain* (Cambridge, MA: MIT Press)
- Clarke D D, Sokoloff L, 1994 "Circulation and energy metabolism of the brain", in *Basic Neurochemistry* Eds G J Siegel, B W Agranoff, R W Albers, P B Molinoff (New York: Raven) pp 645–680
- Corbetta M, Miezin F M, Dobmeyer S, Schulman G L, Petersen S E, 1991 "Selective and divided attention during visual discriminations of shape, color and speed: functional anatomy by positron emission tomography" *Journal of Neuroscience* **11** 2383–2402
- Cowey A, 1979 "Cortical maps and visual perception" *Quarterly Journal of Experimental Psychology* **31** 1–17
- Cragg B G, 1969 "The topography of the afferent projections in the circumstriate visual cortex of the monkey studied by the Nauta method" *Vision Research* **9** 733–747
- Crick F H C, Koch C, 1995 "Are we aware of neural activity in primary visual cortex?" *Nature (London)* **375** 121–123
- Cumming B G, Parker A J, 1997 "Responses of primary visual cortical neurons to binocular disparity without depth perception" *Nature (London)* **389** 280–283
- D'Zmura M, 1991 "Color in visual search" *Vision Research* **31** 951–966
- D'Zmura M, Lennie P, 1986 "Mechanisms of color constancy" *Journal of the Optical Society of America A* **3** 1662–1672
- Daugman J G, 1988 "Complete discrete 2-D Gabor transforms by neural networks for image analysis and compression" *IEEE Transactions on Acoustics, Speech, and Signal Processing* **36** 1169–1179
- De Valois R L, Albrecht D G, Thorell L G, 1982a "Spatial frequency selectivity of cells in macaque visual cortex" *Vision Research* **22** 545–560
- De Valois R L, Yund E W, Helper N, 1982b "The orientation and direction selectivity of cells in macaque visual cortex" *Vision Research* **22** 531–544
- De Weerd P, Desimone R, Ungerleider L G, 1996 "Cue-dependent deficits in grating orientation discrimination after V4 lesions in macaques" *Visual Neuroscience* **13** 529–538
- DeAngelis G C, Anzai A, Ohzawa I, Freeman R D, 1995 "Receptive field structure in the visual cortex: does selective stimulation induce plasticity?" *Proceedings of the National Academy of Sciences of the USA* **92** 9682–9686
- DeAngelis G C, Ohzawa I, Freeman R D, 1991 "Depth is encoded in the visual cortex by a specialized receptive field structure" *Nature (London)* **352** 156–159
- DeAngelis G C, Robson J G, Ohzawa I, Freeman R D, 1992 "Organization of suppression in receptive fields of neurons in cat visual cortex" *Journal of Neurophysiology* **68** 144–163
- DePriest D D, Lennie P, Krauskopf J, 1991 "Slow mechanisms of chromatic adaptation in macaque" *Investigative Ophthalmology & Visual Science* **32** Supplement, 1252
- Derrico J B, Buchsbaum G, 1991 "A computational model of spatiochromatic image coding in early vision" *Journal of Visual Communication and Image Representation* **2** 31–38
- Derrington A M, Lennie P, 1982 "The influence of temporal frequency and adaptation level on receptive field organization of retinal ganglion cells in cat" *Journal of Physiology (London)* **333** 343–366
- Desimone R, 1991 "Face-selective cells in the temporal cortex of monkeys" *Journal of Cognitive Neuroscience* **3** 1–24
- Desimone R, Schein S J, 1987 "Visual properties of neurons in area V4 of the macaque: sensitivity to stimulus form" *Journal of Neurophysiology* **57** 835–868
- Desimone R, Schein S J, Moran J, Ungerleider L G, 1985 "Contour, color and shape analysis beyond the striate cortex" *Vision Research* **25** 441–452

- DeYoe E A, Van Essen D C, 1985 "Segregation of efferent connections and receptive field properties in visual area V2 of the macaque" *Nature (London)* **317** 58–61
- DeYoe E A, Van Essen D C, 1988 "Concurrent processing streams in monkey visual cortex" *Trends in Neuroscience* **11** 219–226
- Douglas R J, Martin K A C, 1991 "Opening the grey box" *Trends in Neuroscience* **14** 286–293
- Dubner R, Zeki S, 1971 "Response properties and receptive fields in an anatomically defined area of the superior temporal sulcus in the monkey" *Brain Research* **35** 528–532
- Duffy C J, Wurtz R H, 1991 "Sensitivity of MST neurons to optic flow stimuli. I. A continuum of response selectivity to large field stimuli" *Journal of Neurophysiology* **65** 1329–1345
- Duffy C J, Wurtz R H, 1995 "Response of monkey MST neurons to optic flow stimuli with shifted centers of motion" *Journal of Neuroscience* **15** 5192–5208
- Durbin R, Mitchison G, 1990 "A dimension reduction framework for understanding cortical maps" *Nature (London)* **343** 644–647
- Edwards D P, Purpura K P, Kaplan E, 1995 "Contrast sensitivity and spatial frequency response of primate cortical neurons in and around the cytochrome oxidase blobs" *Vision Research* **35** 1501–1523
- Engel A K, Knig P, Singer W, 1991 "Direct physiological evidence for scene segmentation by temporal coding" *Proceedings of the National Academy of Sciences of the USA* **88** 9136–9140
- Enroth-Cugell C, Shapley R M, 1973 "Flux, not retinal illumination, is what cat retinal ganglion cells really care about" *Journal of Physiology (London)* **233** 311–326
- Farah M J, 1988 "Is visual imagery really visual? Overlooked evidence from neuropsychology" *Psychological Review* **95** 307–317
- Farah M J, 1990 *Visual Agnosia* (Cambridge, MA: MIT Press)
- Farah M J, Weisberg L L, Monheit M, Peronnet F, 1989 "Brain activity underlying mental imagery: event-related potentials during mental image generation" *Journal of Cognitive Neuroscience* **1** 302–316
- Feldman J A, Ballard D H, 1982 "Connectionist models and their properties" *Cognitive Psychology* **6** 205–254
- Felleman D J, Van Essen D C, 1983 "The connections of area V4 of macaque monkey" *Society for Neuroscience Abstracts* **9** 153
- Felleman D J, Van Essen D C, 1987 "Receptive field properties of neurons in area V3 of macaque monkey extrastriate cortex" *Journal of Neurophysiology* **57** 889–920
- Felleman D J, Van Essen D C, 1991 "Distributed hierarchical processing in the primate cerebral cortex" *Cerebral Cortex* **1** 1–47
- Field D J, 1987 "Relations between the statistics of natural images and the response properties of cortical cells" *Journal of the Optical Society of America A* **4** 2379–2394
- Field D J, 1993 "Scale-invariant and self-similar 'wavelet' transforms: an analysis of natural scenes and mammalian visual systems", in *Wavelets, Fractals, and Fourier Transforms* Eds M Farge, J C R Hunt, J C Vassilicos (Oxford: Clarendon Press) pp 151–193
- Field D J, 1994 "What is the goal of sensory coding?" *Neural Computation* **6** 559–601
- Finke R A, Kosslyn S M, 1980 "Mental imagery acuity in the peripheral visual field" *Journal of Experimental Psychology: Human Perception and Performance* **6** 126–139
- Flanagan P, Cavanagh P, Favreau O E, 1990 "Independent orientation-selective mechanisms for the cardinal directions of colour space" *Vision Research* **30** 769–778
- Foster K H, Gaska J P, Nagler M, Pollen D A, 1985 "Spatial and temporal frequency selectivity of neurones in visual cortical areas V1 and V2 of the macaque monkey" *Journal of Physiology (London)* **365** 331–363
- Freeman R D, Ohzawa I, 1990 "On the neurophysiological organization of binocular vision" *Vision Research* **30** 1661–1676
- Gallant J, Braun J, Van Essen D C, 1993 "Selectivity for polar, hyperbolic, and Cartesian gratings in macaque visual cortex" *Science* **259** 100–103
- Garey L J, Powell T P S, 1971 "An experimental study of the termination of the lateral geniculocortical pathway in the cat and monkey" *Proceedings of the Royal Society of London B* **179** 41–63
- Gattass R, Gross C G, Sandell J H, 1981 "Visual topography of V2 in the macaque" *Journal of Comparative Neurology* **201** 519–539
- Gattass R, Sousa A P B, Gross C G, 1988 "Visuotopic organization and extent of V3 and V4 of macaque" *Journal of Neuroscience* **8** 1831–1845
- Gegenfurtner K R, Kiper D C, Fenstemaker S B, 1996 "Processing of color, form, and motion in macaque area V2" *Visual Neuroscience* **13** 161–172

- Gegenfurtner K R, Kiper D C, Levitt J B, 1997 "Functional properties of neurons in macaque area V3" *Journal of Neurophysiology* **77** 1906–1923
- Geisler W S, Albrecht D G, 1995 "Bayesian analysis of identification performance in monkey visual cortex: nonlinear mechanisms and stimulus certainty" *Vision Research* **35** 2723–2730
- Ghose G M, Freeman R D, 1992 "Oscillatory discharge in the visual system: does it have a functional role?" *Journal of Neurophysiology* **68** 1558–1574
- Ghose G M, Freeman R D, 1997 "Intracortical connections are not required for oscillatory activity in the visual cortex" *Visual Neuroscience* **14** 963–979
- Gilbert C D, 1992 "Horizontal integration and cortical dynamics" *Neuron* **9** 1–13
- Gilbert C D, Wiesel T N, 1983 "Clustered intrinsic connections in cat visual cortex" *Journal of Neuroscience* **3** 1116–1133
- Gilbert C D, Wiesel T N, 1989 "Columnar specificity of intrinsic horizontal and cortico-cortical connections in cat visual cortex" *Journal of Neuroscience* **9** 2432–2442
- Gilbert C D, Wiesel T N, 1990 "The influence of contextual stimuli on the orientational selectivity of cells in primary visual cortex of the cat" *Vision Research* **30** 1689–1701
- Gilbert C D, Wiesel T N, 1992 "Receptive field dynamics in adult primary visual cortex" *Nature (London)* **356** 150–152
- Goldenberg G, Podreka I, Steiner M, Willmes K, 1987 "Patterns of regional cerebral blood flow related to memorizing high and low imagery words—an emission computer tomography study" *Neuropsychologia* **25** 473–486
- Graham N, 1989 *Visual Pattern Analyzers* (New York: Oxford University Press)
- Graham N, Sutter A, Venkatesan C, 1993 "Spatial-frequency- and orientation-selectivity of simple and complex channels in region segregation" *Vision Research* **33** 1893–1911
- Gray C M, Knig P, Engel A K, Singer W, 1989 "Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties" *Nature (London)* **338** 334–337
- Grosfod D H, Shapley R M, Hawken M J, 1993 "Macaque V1 neurons can respond to illusory contours" *Nature (London)* **365** 550–552
- Gross C G, Rocha-Miranda C E, Bender D B, 1972 "Visual properties of neurons in inferotemporal cortex of the macaque" *Journal of Neurophysiology* **35** 96–111
- Grüsser O J, Landis T, 1991 *Visual Agnosias and Other Disturbances of Visual Perception and Cognition* (Boca Raton, FL: CRC Press)
- Gulyas B, Lagae L, Eysel U, Orban G, 1990 "Corticofugal feedback influences the responses of geniculate neurons to moving stimuli" *Experimental Brain Research* **79** 441–446
- Gulyas B, Orban G A, Duysens J, Maes H, 1987 "The suppressive influence of moving texture background on responses of cat striate cortex to moving bars" *Journal of Neurophysiology* **57** 1767–1791
- Haenny P E, Schiller P H, 1988 "State dependent activity in monkey visual cortex. I. Single cell activity in V1 and V4 on visual tasks" *Experimental Brain Research* **69** 225–244
- Hammond P, MacKay D M, 1977 "Differential responsiveness of simple and complex cells in striate cortex to visual texture" *Experimental Brain Research* **30** 275–296
- Hancock P J B, Baddeley R J, Smith L S, 1992 "The principal components of natural images" *Network* **3** 61–70
- Harwerth R S, 1986 "Multiple sensitive periods in the development of the primate visual system" *Science* **232** 235–238
- Hawken M J, Parker A J, 1987 "Spatial properties of neurons in the monkey striate cortex" *Proceedings of the Royal Society of London B* **231** 251–288
- Hawken M J, Parker A J, Lund J S, 1988 "Laminar organization and contrast sensitivity of direction-selective cells in the striate cortex of the old world monkey" *Journal of Neuroscience* **8** 3541–3548
- Heeger D J, 1992a "Half-squaring in responses of cat striate cells" *Visual Neuroscience* **9** 427–443
- Heeger D J, 1992b "Normalization of cell responses in cat striate cortex" *Visual Neuroscience* **9** 181–197
- Heinen S J, Skavenski A A, 1991 "Recovery of visual responses in foveal V1 neurons following bilateral foveal lesions in adult monkey" *Experimental Brain Research* **83** 670–674
- Hess R F, Baker C L Jr, Zihl J, 1989 "The 'motion-blind' patient: low-level spatial and temporal filters" *Journal of Neuroscience* **9** 1628–1640
- Heydt R von der, Peterhans E, 1989 "Mechanisms of contour perception in monkey visual cortex. I. Lines of pattern discontinuity" *Journal of Neuroscience* **9** 1731–1748
- Heywood C A, Cowey A, 1987 "On the role of cortical visual area V4 in the discrimination of hue and pattern in macaque monkeys" *Journal of Neuroscience* **7** 2601–2616

- Heywood C A, Gadotti A, Cowey A, 1992 "Cortical area V4 and its role in the perception of color" *Journal of Neuroscience* **12** 4056–4065
- Hilgetag C-C, O'Neill M A, Young M P, 1996 "Indeterminate organization of the visual system" *Science* **271** 776–777
- Hinton G E, Dayan P, Frey B J, Neal R M, 1995 "The 'wake-sleep' algorithm for unsupervised neural networks" *Science* **268**
- Hinton G E, McClelland J L, Rumelhart D E, 1986 "Distributed representations", in *Parallel Distributed Processing Volume 1 Foundations* Eds D E Rumelhart, J L McClelland (Cambridge, MA: MIT Press) pp 77–109
- Holmes G, 1918 "Disturbances of vision by cerebral lesions" *British Journal of Ophthalmology* **2** 353–384
- Hopfield J J, 1995 "Pattern recognition computing using action potential timing for stimulus representation" *Nature (London)* **376** 33–36
- Horton J C, Hoyt W F, 1991 "Quadratic visual field defects" *Brain* **114** 1703–1718
- Horton J C, Hubel D H, 1981 "A regular patchy distribution of cytochrome-oxidase staining in primary visual cortex of the macaque monkey" *Nature (London)* **292** 762–764
- Hubel D H, Livingstone M S, 1987 "Segregation of form color and stereopsis in primate area 18" *Journal of Neuroscience* **7** 3378–3415
- Hubel D H, Wiesel T N, 1962 "Receptive fields, binocular interactions, and functional architecture in the cat's visual cortex" *Journal of Physiology (London)* **160** 106–154
- Hubel D H, Wiesel T N, 1965 "Receptive fields and functional architecture in two nonstriate visual areas (18 and 19) of the cat" *Journal of Neurophysiology* **28** 229–289
- Hubel D H, Wiesel T N, 1968 "Receptive fields and functional architecture of monkey striate cortex" *Journal of Physiology (London)* **195** 215–243
- Hubel D H, Wiesel T N, 1970 "Cells sensitive to binocular depth in area 18 of the macaque cortex" *Nature (London)* **225** 41–42
- Hubel D H, Wiesel T N, 1974 "Uniformity of monkey striate cortex: a parallel relationship between field size, scatter, and magnification factor" *Journal of Comparative Neurology* **158** 295–306
- Hubel D H, Wiesel T N, 1977 "The Ferrier lecture. Functional architecture of macaque monkey visual cortex" *Proceedings of the Royal Society of London B* **198** 1–59
- Jones E G, Wise S P, 1977 "Size, laminar and columnar distribution of efferent cells in the sensory-motor cortex of monkeys" *Journal of Comparative Neurology* **175** 391–437
- Kaas J H, Krubitzer L A, Chino Y M, Langston A L, Polley E H, Blair N, 1990 "Reorganization of the retinotopic cortical maps in adult mammals after lesions of the retina" *Science* **248** 229–231
- Kanerva P, 1988 *Sparse Distributed Memory* (Cambridge, MA: MIT Press)
- Kersten D, 1987 "Predictability and redundancy of natural images" *Journal of the Optical Society of America A* **4** 2395–2400
- Kiper D C, Fenstemaker S B, Gegenfurtner K R, 1997 "Chromatic properties of neurons in macaque area V2" *Visual Neuroscience* **14** 1061–1072
- Knierim J J, Van Essen D C, 1992 "Neuronal responses to static texture patterns in area V1 of the alert macaque monkey" *Journal of Neurophysiology* **67** 961–980
- Koenderink J J, 1986 "Optic flow" *Vision Research* **26** 161–180
- Kosslyn S M, Thompson W L, Kim I J, Alpert N M, 1995 "Topographical representations of mental images in primary visual cortex" *Nature (London)* **378** 496–508
- Krüger J, Gouras P, 1980 "Spectral selectivity of cells and its dependence on slit length in monkey visual cortex" *Journal of Neurophysiology* **43** 1055–1069
- Lamme V A F, 1995 "The neurophysiology of figure-ground segregation in primary visual cortex" *Journal of Neuroscience* **15** 1605–1615
- Lehky S R, Maunsell J H, 1996 "No binocular rivalry in the LGN of alert macaque monkeys" *Vision Research* **36** 1225–1234
- Lehky S R, Sejnowski T J, 1988 "Network model of shape-from-shading: neural function arises from both receptive and projective fields" *Nature (London)* **331** 679–684
- Lennie P, Krauskopf J, Sclar G, 1990a "Chromatic mechanisms in striate cortex of macaque" *Journal of Neuroscience* **10** 649–669
- Lennie P, Trevarthen C, Van Essen D, Wässle H, 1990b "Parallel processing of visual information", in *Visual Perception: The Neurophysiological Foundations* Eds L Spillmann, J Werner (New York: Academic Press) pp 103–128
- Leopold D A, Logothetis N K, 1996 "Activity changes in early visual cortex reflect monkeys' percepts during binocular rivalry" *Nature (London)* **379** 549–553

- Lettvin J Y, Maturana H R, McCulloch W S, Pitts W H, 1959 "What the frog's eye tells the frog's brain" *Proceedings of the Institute of Radio Engineers* **47** 1940–1951
- Leventhal A G, Thompson K G, Liu D, Zhou Y, Ault S J, 1995 "Concomitant sensitivity to orientation, direction, and color of cells in layers 2, 3, and 4 of monkey striate cortex" *Journal of Neuroscience* **15** 1808–1818
- Levitt J B, Kiper D C, Movshon J A, 1994 "Receptive fields and functional architecture of macaque V2" *Journal of Neurophysiology* **71** 2517–2542
- Levitt J B, Lund J S, 1997 "Contrast dependence of contextual effects in primate visual cortex" *Nature (London)* **387** 73–76
- Livingstone M S, 1996 "Oscillatory firing and interneuronal correlations in squirrel monkey striate cortex" *Journal of Neurophysiology* **75** 2467–2485
- Livingstone M S, Hubel D H, 1984a "Anatomy and physiology of a color system in the primate visual cortex" *Journal of Neuroscience* **4** 309–356
- Livingstone M S, Hubel D H, 1984b "Specificity of intrinsic connections in primate primary visual cortex" *Journal of Neuroscience* **4** 2830–2835
- Livingstone M S, Hubel D H, 1987 "Psychophysical evidence for separate channels for the perception of form, color, movement, and depth" *Journal of Neuroscience* **7** 3416–3468
- Livingstone M S, Hubel D H, 1988 "Segregation of form, color, movement, and depth: anatomy, physiology and perception" *Science* **240** 740–749
- Logothetis N K, Leopold D A, Sheinberg D L, 1996 "What is rivaling during binocular rivalry?" *Nature (London)* **380** 621–624
- Logothetis N K, Pauls J, Bülthoff H H, Poggio T, 1994 "View-dependent object recognition by monkeys" *Current Biology* **4** 401–414
- Lund J S, Lund R D, Hendrickson A E, Bunt A H, Fuchs A F, 1975 "The origin of efferent pathways from the primary visual cortex, area 17, of the macaque monkey as shown by retrograde transport of horseradish peroxidase" *Journal of Comparative Neurology* **164** 287–304
- McClurkin J W, Optican L M, Richmond B J, 1994 "Cortical feedback increases visual information transmitted by monkey parvocellular lateral geniculate nucleus neurons" *Visual Neuroscience* **11** 601–617
- McCollough C, 1965 "Color adaptation of edge detectors in the human visual system" *Science* **149** 1115–1116
- McGuire B A, Gilbert C D, Rivlin P K, Wiesel T N, 1991 "Targets of horizontal connections in macaque primary visual cortex" *Journal of Comparative Neurology* **305** 370–392
- Maffei L, Fiorentini A, 1976 "The unresponsive regions of visual cortical receptive fields" *Vision Research* **16** 1131–1139
- Maguire W M, Baizer J S, 1984 "Visuotopic organization of the prelunate gyrus in rhesus monkey" *Journal of Neuroscience* **4** 1690–1704
- Maloney L T, 1986 "Evaluation of linear models of surface spectral reflectance with small numbers of parameters" *Journal of the Optical Society of America A* **3** 1673–1683
- Marr D, 1982 *Vision: A Computational Investigation into the Human Representation and Processing of Visual Information* (San Francisco, CA: W H Freeman)
- Marr D, Hildreth E, 1980 "Theory of edge detection" *Proceedings of the Royal Society of London B* **207** 187–217
- Marrocco R T, McClurkin J W, Young R A, 1982 "Modulation of lateral geniculate nucleus cell responsiveness by visual activation of the corticogeniculate pathway" *Journal of Neuroscience* **2** 256–263
- Marshall J C, Halligan P W, 1995 "Seeing the forest but only half the trees" *Nature (London)* **373** 521–523
- Matsubara J A, Cynader M S, Swindale N V, 1987 "Anatomical properties and physiological correlates of the intrinsic connections in cat area 18" *Journal of Neuroscience* **7** 1428–1446
- Maunsell J H R, Van Essen D C, 1983 "The connections of the middle temporal visual area (MT) and their relationship to a cortical hierarchy in the macaque monkey" *Journal of Neuroscience* **3** 2563–2586
- Maunsell J H R, Gibson J R, 1992 "Visual response latencies in striate cortex of the macaque monkey" *Journal of Neurophysiology* **68** 1332–1344
- Maunsell J H R, Van Essen D C, 1987 "Topographic organization of the middle temporal visual area in the macaque monkey: representation biases and the relationship to callosal connections and myeloarchitectonic boundaries" *Journal of Comparative Neurology* **266** 535–555
- Merigan W H, 1996 "Basic visual capacities and shape discrimination after lesions of extrastriate area V4 in macaques" *Visual Neuroscience* **13** 51–60

- Merigan W H, Maunsell J H R, 1993 "How parallel are the primate visual pathways?" *Annual Review of Neuroscience* **16** 369–402
- Merigan W H, Nealey T A, Maunsell J H R, 1993 "Visual effects of lesions of cortical area V2 in macaques" *Journal of Neuroscience* **13** 3180–3191
- Mitchison G, 1991 "Neuronal branching patterns and the economy of cortical wiring" *Proceedings of the Royal Society of London B* **245** 151–158
- Mollon J D, Newcombe F, Polden P G, Ratcliff G, 1980 "On the presence of three cone mechanisms in a case of total achromatopsia", in *Colour Vision Deficiencies* Ed. G Verriest (Bristol: Hilger) pp 130–135
- Moran J, Desimone R, 1985 "Selective attention gates visual performance in the extrastriate cortex" *Science* **229** 782–784
- Morrone M C, Burr D C, 1988 "Feature detection in human vision: a phase dependent energy model" *Proceedings of the Royal Society of London B* **235** 221–245
- Morrone M C, Burr D C, Maffei L, 1982 "Functional implications of cross-orientation inhibition of cortical visual cells. I. Neurophysiological evidence" *Proceedings of the Royal Society of London B* **216** 335–354
- Motter B C, 1993 "Focal attention produces spatially selective processing in visual cortical areas V1, V2 and V4 in the presence of competing stimuli" *Journal of Neurophysiology* **70** 909–919
- Motter B C, 1994a "Neural correlates of attentive selection for color or luminance in extrastriate area V4" *Journal of Neuroscience* **14** 2178–2199
- Motter B C, 1994b "Neural correlates of feature-selective memory and pop-out in extrastriate area V4" *Journal of Neuroscience* **14** 2190–2199
- Movshon J A, Adelson E H, Gizzi M S, Newsome W H, 1985 "The analysis of moving visual patterns", in *Pattern Recognition Mechanisms* Eds C Chagas, R Gattass, C Gross (New York: Springer) pp 117–151
- Movshon J A, Lennie P, 1979 "Pattern-selective adaptation in visual cortical neurones" *Nature (London)* **278** 850–852
- Movshon J A, Thompson I D, Tolhurst D J, 1978 "Receptive field organization of complex cells in the cat's striate cortex" *Journal of Physiology (London)* **283** 79–99
- Müller J R, Singer B, Krauskopf J, Lennie P, 1996 "Center-surround contrast effects in macaque cortex" *Investigative Ophthalmology & Visual Science* **37**(4) S904
- Mumford D, 1994 "Neuronal architectures for pattern-theoretic problems", in *Large-Scale Neuronal Theories of the Brain* Eds K Koch, J L Davis (Cambridge, MA: MIT Press) pp 125–152
- Murphy P C, Sillito A M, 1987 "Corticofugal feedback influences the generation of length tuning in the visual pathway" *Nature (London)* **329** 727–729
- Nakayama K, Silverman G H, 1986 "Serial and parallel processing of visual feature conjunctions" *Nature (London)* **320** 264–265
- Nelson J I, Frost B J, 1978 "Orientation-selective inhibition from beyond the classical receptive field" *Brain Research* **139** 359–365
- Nelson J I, Frost B J, 1985 "Intracortical facilitation among co-oriented, co-axially aligned simple cells in cat striate cortex" *Experimental Brain Research* **61** 54–61
- Newsome W T, Paré E B, 1988 "A selective impairment of motion perception following lesions of the middle temporal visual area (MT)" *Journal of Neuroscience* **8** 2201–2211
- Newsome W T, Wurtz R H, Dürsteler M R, Mikami A, 1985 "Deficits in visual motion processing following ibotenic acid lesions of the middle temporal visual area" *Journal of Neuroscience* **5** 825–840
- Nothdurft H C, Li C Y, 1985 "Texture discrimination: representation of orientation and luminance differences in cells of the cat striate cortex" *Vision Research* **25** 99–114
- Nowak L G, Munk M H J, Girard P, Bullier J, 1995 "Visual latencies in areas V1 and V2 of the macaque monkey" *Visual Neuroscience* **12** 371–384
- O'Kusky J, Colonnier M, 1982 "A laminar analysis of the number of neurons, glia, and synapses in the visual cortex (area 17) of adult macaque monkeys" *Journal of Comparative Neurology* **210** 278–290
- Ohzawa I, Freeman R D, 1986a "The binocular organization of simple cells in the cat's visual cortex" *Journal of Neurophysiology* **56** 221–242
- Ohzawa I, Freeman R D, 1986b "The binocular organization of complex cells in the cat's visual cortex" *Journal of Neurophysiology* **56** 243–259
- Ohzawa I, Sclar G, Freeman R D, 1985 "Contrast gain control in the cat's visual system" *Journal of Neurophysiology* **54** 651–667

- Optican L M, Richmond B J, 1987 "Temporal encoding of two-dimensional patterns by single units in primate inferior temporal cortex. III. Information theoretic analysis" *Journal of Neurophysiology* **57** 162–178
- Oram M W, Perett D I, 1992 "Time course of neural responses discriminating different views of the face and the head" *Journal of Neurophysiology* **68** 70–84
- Orban G A, Gulys B, Vogels R, 1987 "Influence of moving textured background on direction selectivity of cat striate neurons" *Journal of Neurophysiology* **57** 1792–1812
- Orban G A, Kennedy H, Bullier J, 1986 "Velocity sensitivity and direction selectivity of neurons in areas V1 and V2 of the monkey: influence of eccentricity" *Journal of Neurophysiology* **56** 462–480
- Palmer J, 1994 "Set-size effects in visual search: the effect of attention is independent of the stimulus for simple tasks" *Vision Research* **34** 1703–1721
- Parker A J, Hawken M J, 1985 "Capabilities of monkey cortical cells in spatial-resolution tasks" *Journal of the Optical Society of America A* **2** 1101–1114
- Penfield W, Rasmussen T, 1950 *The Cerebral Cortex of Man* (New York: Macmillan)
- Perrett D I, Mistlin A J, Chitty A J, 1987 "Visual neurones responsive to faces" *Trends in Neuroscience* **10** 358–364
- Peterhans E, Heydt R von der, 1989 "Mechanisms of contour perception in monkey visual cortex. II. Contours bridging gaps" *Journal of Neuroscience* **9** 1749–1763
- Peterhans E, Heydt R von der, 1993 "Functional organization of area V2 in the alert monkey" *European Journal of Neuroscience* **5** 509–524
- Phillips G C, Zeki S M, Barlow H B, 1984 "Localisation of function in the cerebral cortex: past, present and future" *Brain* **107** 327–361
- Poggio G F, Fischer B, 1977 "Binocular interaction and depth sensitivity in striate and prestriate cortex of behaving rhesus monkey" *Journal of Neurophysiology* **40** 1392–1405
- Poggio G F, Gonzalez F, Krause F, 1988 "Stereoscopic mechanisms in monkey visual cortex: binocular correlation and disparity selectivity" *Journal of Neuroscience* **8** 4531–4550
- Powell T P S, Hendrickson A E, 1981 "Similarity in the number of neurons through the depth of the cortex in the binocular and monocular parts of area 17 of the monkey" *Brain Research* **216** 409–413
- Robson J A, 1983 "The morphology of corticofugal axons to the dorsal lateral geniculate nucleus in the cat" *Journal of Comparative Neurology* **216** 89–103
- Robson J G, 1980 "Neural images: the physiological basis of spatial vision", in *Visual Coding and Adaptability* Ed. C S Harris (Hillsdale, NJ: Lawrence Erlbaum Associates) pp 177–214
- Robson J G, 1988 "Linear and non-linear operations in the visual system" *Investigative Ophthalmology & Visual Science* **29** Supplement, 117
- Rock I, 1986 "The description and analysis of object and event perception", in *Handbook of Perception and Human Performance* Eds K R Boff, L R Kaufman, J P Thomas (New York: John Wiley) pp 33:1–33:71
- Rockel A J, Hiorns R W, Powell T P S, 1980 "The basic uniformity in structure of the neocortex" *Brain* **103** 221–244
- Rockland K S, Lund J S, 1983 "Intrinsic laminar lattice connections in primate visual cortex" *Journal of Comparative Neurology* **216** 303–318
- Rockland K S, Pandya D N, 1979 "Laminar origins and terminations of cortical connections of the occipital lobe in the rhesus monkey" *Brain Research* **179** 3–20
- Rodieck R W, 1988 "The primate retina", in *Comparative Primate Biology* (New York: Alan R Liss) pp 203–278
- Roe A W, Ts'o D Y, 1995 "Visual topography in primate V2: multiple representation across functional stripes" *Journal of Neuroscience* **15** 3689–3715
- Roland P E, Friberg L, 1985 "Localization of cortical areas activated by thinking" *Journal of Neurophysiology* **53** 1219–1243
- Roland P E, Gulys B, 1994 "Visual imagery and visual representation" *Trends in Neuroscience* **17** 281–287
- Rolls E T, 1992 "Neurophysiological mechanisms underlying face processing within and beyond the temporal cortical visual areas" *Philosophical Transactions of the Royal Society of London B* **335** 11–21
- Sacks O, Wasserman R, Zeki S M, Siegel R M, 1988 "Sudden color-blindness of cerebral origin" *Society for Neuroscience Abstracts* **14** 1251
- Saito H, Tanaka K, Isono H, Yasuda M, Mikami A, 1989 "Directionally selective response of cells in the middle temporal area (MT) of the macaque monkey to the movement of equi-luminous opponent colour stimuli" *Experimental Brain Research* **75** 1–14

- Sakitt B, Barlow H B, 1982 "A model for the economical encoding of the visual image in cerebral cortex" *Biological Cybernetics* **43** 97–108
- Salzman C D, Murasugi C M, Britten K H, Newsome W T, 1992 "Microstimulation in visual area MT: effects on direction discrimination performance" *Journal of Neuroscience* **12** 2331–2355
- Schein S J, Desimone R, 1990 "Spectral properties of V4 neurons in the macaque" *Journal of Neuroscience* **10** 3369–3389
- Schein S J, Marrocco R T, Monasterio F M de, 1982 "Is there a high concentration of color-selective cells in area V4 of monkey visual cortex?" *Journal of Neurophysiology* **47** 193–213
- Schiller P, 1993 "The effects of V4 and middle temporal (MT) area lesions on visual performance in the rhesus monkey" *Visual Neuroscience* **10** 717–746
- Sciar G, Lennie P, DePriest D D, 1989 "Contrast adaptation in striate cortex of macaque" *Vision Research* **29** 747–755
- Sciar G, Maunsell J H R, Lennie P, 1990 "Coding of image contrast in central visual pathways of the macaque monkey" *Vision Research* **30** 1–10
- Sengpiel F, Blakemore C, Harrad R, 1995 "Interocular suppression in primary visual cortex: a possible neural basis of binocular rivalry" *Vision Research* **35** 179–195
- Shapley R, 1990 "Visual sensitivity and parallel retinocortical channels" *Annual Review of Psychology* **41** 635–658
- Shapley R M, Victor J D, 1986 "Hyperacuity in cat retinal ganglion cells" *Science* **31** 999–1002
- Shipp S, Zeki S M, 1985 "Segregation of pathways leading from area V2 to areas V4 and V5 of macaque monkey visual cortex" *Nature (London)* **315** 322–325
- Sillito A M, Grieve K L, Jones H E, Cudeiro J, Davis J, 1995 "Visual cortical mechanisms detecting focal orientation discontinuities" *Nature (London)* **378** 492–496
- Silveira L C L, Perry V H, 1990 "The topography of magnocellular projecting ganglion cells (M-ganglion cells) in the primate retina" *Neuroscience* **40** 217–237
- Silverman M S, Grosf D H, De Valois R L, Elfar S D, 1989 "Spatial-frequency organization in primate striate cortex" *Proceedings of the National Academy of Sciences of the USA* **86** 711–715
- Singer W, 1993 "Synchronization of cortical activity and its putative role in information processing and learning" *Annual Review of Physiology* **55** 349–374
- Skowbo D, Timney B N, Gentry T H, Morant R B, 1975 "McCollough effects: experimental findings and theoretical accounts" *Psychological Bulletin* **82** 497–510
- Spitzer H, Hochstein S, 1985 "A complex-cell receptive field model" *Journal of Neurophysiology* **53** 1266–1286
- Srinivasan M V, Laughlin S B, Dubs A, 1982 "Predictive coding: a fresh view of lateral inhibition in the retina" *Proceedings of the Royal Society of London B* **216** 427–459
- Stoner G R, Albright T D, 1992 "Neural correlates of perceptual motion coherence" *Nature (London)* **358** 412–414
- Swindale N V, 1992 "A model for the coordinated development of columnar systems in primate striate cortex" *Biological Cybernetics* **66** 217–230
- Tanaka M, Lindsley E, Lausmann S, Creutzfeldt O, 1990 "Afferent connections of the prelunate visual association cortex (areas V4 and DP)" *Anatomy and Embryology* **181** 19–30
- Thorell L G, De Valois R L, Albrecht D G, 1984 "Spatial mapping of monkey V1 cells with pure color and luminance stimuli" *Vision Research* **24** 751–769
- Thorpe S J, Imbert M, 1989 "Biological constraints on connectionist modelling", in *Connectionism in Perspective* Eds R Pfeifer, Z Schreier, F Fogelman-Soulié, L Steels (Amsterdam: Elsevier) pp 63–92
- Tolhurst D J, Tadmor Y, Tang C, 1992 "The amplitude spectra of natural images" *Ophthalmic and Physiological Optics* **12** 229–232
- Tootell R B H, Hamilton S L, 1989 "Functional anatomy of the second visual area (V2) in the macaque" *Journal of Neuroscience* **9** 2620–2644
- Tootell R B H, Silverman M S, De Valois R L, Jacobs G H, 1983 "Functional organization of the second cortical visual area (V2) in the primate" *Science* **220** 737–739
- Tootell R B H, Silverman M S, Hamilton S L, De Valois R L, Switkes E, 1988a "Functional anatomy of macaque striate cortex III. Color" *Journal of Neuroscience* **8** 1569–1593
- Tootell R B H, Silverman M S, Hamilton S L, Switkes E, De Valois R L, 1988b "Functional anatomy of macaque striate cortex V. Spatial frequency" *Journal of Neuroscience* **8** 1610–1624
- Tovée M J, Rolls E T, Treves A, Bellis R P, 1993 "Information encoding and the responses of single neurons in the primate temporal visual cortex" *Journal of Neurophysiology* **70** 640–654
- Treisman A M, 1986 "Properties, parts, and objects", in *Handbook of Perception and Human Performance* Eds K R Boff, L R Kaufman, J P Thomas (New York: John Wiley) pp 35:1–35:70

- Treisman A M, 1988 "Features and objects: the fourteenth Bartlett memorial lecture" *Quarterly Journal of Experimental Psychology A* **40** 201–237
- Treisman A M, Gelade G, 1980 "A feature integration theory of attention" *Cognitive Psychology* **12** 97–136
- Treisman A M, Gormican S, 1988 "Feature analysis in early vision: evidence from search symmetries" *Psychological Review* **95** 15–48
- Treue S, Maunsell J H, 1996 "Attentional modulation of visual motion processing in cortical areas MT and MST" *Nature (London)* **382** 539–541
- Ts'o D Y, Frostig R D, Lieke E E, Grinvald A, 1990 "Functional organization of primate visual cortex revealed by high resolution optical imaging" *Science* **249** 417–420
- Ts'o D Y, Gilbert C D, 1988 "The organization of chromatic and spatial interactions in the primate striate cortex" *Journal of Neuroscience* **8** 1712–1727
- Ts'o D Y, Gilbert C D, Wiesel T N, 1986 "Relationships between horizontal interactions and functional architecture in cat striate cortex as revealed by cross-correlation analysis" *Journal of Neuroscience* **6** 1160–1170
- Ullman S, 1992 "Low-level aspects of segmentation and recognition" *Philosophical Transactions of the Royal Society of London B* **337** 371–379
- Ungerleider L G, Mishkin M, 1982 "Two cortical visual systems", in *Analysis of Visual Behavior* Eds D J Ingle, M A Goodale, R W J Mansfield (Cambridge, MA: MIT Press) pp 549–586
- Van Essen D C, Felleman D J, DeYoe E A, Olavarria J, Knierim J, 1990 "Modular and hierarchical organization of extrastriate visual cortex in the macaque monkey" *Cold Spring Harbor Symposium on Quantitative Biology* **55** 679–685
- Van Essen D C, Maunsell J H R, Bixby J L, 1981 "The middle temporal visual area in the macaque: myeloarchitecture, connections, functional properties and topographic organization" *Journal of Comparative Neurology* **199** 293–326
- Van Essen D C, Newsome W T, Maunsell J H R, 1984 "The visual field representation in striate cortex of the macaque monkey: asymmetries, anisotropies, and individual variability" *Vision Research* **24** 429–448
- Van Essen D C, Newsome W T, Maunsell J H R, Bixby J L, 1986 "The projections from striate cortex (V1) to areas V2 and V3 in the macaque monkey: asymmetries, areal boundaries, and patchy connections" *Journal of Comparative Neurology* **244** 451–480
- Vautin R G, Berkley M A, 1977 "Responses of single cells in cat visual cortex to prolonged stimulus movement: neural correlates of visual aftereffects" *Journal of Neurophysiology* **40** 1051–1065
- Vautin R G, Dow B M, 1985 "Color cell groups in foveal striate cortex of the behaving macaque" *Journal of Neurophysiology* **54** 273–292
- Vergheze P, Nakayama K, 1994 "Stimulus discriminability in visual search" *Vision Research* **34** 2453–2467
- Victor J D, Maiese K, Shapley R, Sidtis J, Gazzaniga M S, 1989 "Acquired central dyschromatopsia: analysis of a case with preservation of color discrimination" *Clinical Vision Sciences* **4** 183–196
- Vogels R, 1990 "Population coding of stimulus orientation by striate cortical cells" *Biological Cybernetics* **64** 25–31
- Watson A B, 1987 "Efficiency of a model human image code" *Journal of the Optical Society of America A* **4** 2401–2417
- Watson A B, 1990 "Algotecture of visual cortex", in *Vision: Coding and Efficiency* Ed. C Blakemore (Cambridge: Cambridge University Press) pp 393–410
- Watt R J, Morgan M J, 1984 "Spatial filters and the localization of luminance changes in human vision" *Vision Research* **24** 1387–1398
- Whittle P, Bloor D C, Pocock S, 1968 "Some experiments on figural effects in binocular rivalry" *Perception & Psychophysics* **4** 183–188
- Willshaw D J, 1981 "Holography, associative memory, and inductive generalization", in *Parallel Models of Associative Memory* Eds G Hinton, J A Anderson (Hillsdale, NJ: Lawrence Erlbaum Associates) pp 83–104
- Wilson M E, Cragg B G, 1967 "Projections from the lateral geniculate nucleus in the cat and monkey" *Journal of Anatomy* **101** 677–692
- Wolfe J M, Cave K R, Franzel S L, 1989 "Guided search, an alternative to the feature integration theory for visual search" *Journal of Experimental Psychology: Human Perception and Performance* **15** 419–433
- Young M P, 1992 "Objective analysis of the topological organization of the primate cortical visual system" *Nature (London)* **358** 152–155

-
- Young M P, Tanaka K, Yamane S, 1992 "On oscillating neuronal responses in the visual cortex of the monkey" *Journal of Neurophysiology* **67** 1464–1474
- Zeki S M, 1969 "Representation of central visual fields in prestriate cortex of monkey" *Brain Research* **14** 271–291
- Zeki S M, 1971 "Cortical projections from two prestriate areas in the monkey" *Brain Research* **34** 19–35
- Zeki S M, 1973 "Colour coding in rhesus monkey prestriate cortex" *Brain Research* **53** 422–427
- Zeki S M, 1974 "Cells responding to changing size and disparity in the cortex of the rhesus monkey" *Journal of Physiology (London)* **242** 827–841
- Zeki S M, 1978a "The cortical projections of foveal striate cortex in the rhesus monkey" *Journal of Physiology (London)* **277** 227–244
- Zeki S M, 1978b "Functional specialization in the visual cortex of the rhesus monkey" *Nature (London)* **274** 423–428
- Zeki S M, 1978c "The third visual complex of rhesus monkey prestriate cortex" *Journal of Physiology (London)* **277** 245–272
- Zeki S M, 1978d "Uniformity and diversity of structure and function in rhesus monkey prestriate visual cortex" *Journal of Physiology (London)* **277** 273–290
- Zeki S M, 1983a "Colour coding in the cerebral cortex: the reaction of cells in monkey visual cortex to wavelengths and colours" *Neuroscience* **9** 741–765
- Zeki S M, 1983b "Colour coding in the cerebral cortex: the responses of wavelength-selective and colour-coded cells in monkey visual cortex to changes in wavelength composition" *Neuroscience* **9** 767–781
- Zeki S M, 1990 "A century of cerebral achromatopsia" *Brain* **113** 1721–1777
- Zeki S M, Shipp S, 1988 "The functional logic of cortical connections" *Nature (London)* **335** 311–317
- Zeki S M, Watson J D G, Lueck C J, Friston K J, Kennard C, Frackowiak R S J, 1991 "A direct demonstration of functional specialization in human visual cortex" *Journal of Neuroscience* **11** 641–649
- Zihl J, Cramon D von, Mai N, 1983 "Selective disturbance of movement vision after bilateral brain damage" *Brain* **106** 313–340
- Zipser K, Lee T-S, Lamme V A F, Schiller P H, 1994 "Invariance of figure-ground segregation mechanisms in V1 for depth, orientation, luminance, and chrominance cues" *Investigative Ophthalmology & Visual Science* **35**(4) 1973
- Zohary E, 1992 "Population coding of visual stimuli by cortical neurons tuned to more than one dimension" *Biological Cybernetics* **66** 265–272