7

The Functional Architecture of Area V2 in the Macaque Monkey

Physiology, Topography, and Connectivity

ANNA WANG ROE and DANIEL Y. TS'O

1. Introduction

One of the most striking aspects of the primate visual cortex is the remarkable extent of internal structure and organization within V1, and the second visual area, V2. Architecturally, V2 is composed of an interleaved series of bands specialized for the processing of the visual submodalities of form, color, and depth, known as the V2 stripes. The unique position of V2 in the visual hierarchy at the juncture of the higher visual pathways suggests that its segregated functional architecture facilitates the channeling of visual input into these pathways for handling "what" and "where" visual information. Thus the organization and connectivity of V2 perhaps most clearly embodies the notion of parallel and integrated processing of form, color, motion, and stereopsis, as observed psychophysically in studies of human visual performance. In comparison to primary visual cortex V1, the architecture and functional role of V2 has only recently been studied in earnest. This chapter reviews the current understand-

ANNA WANG ROE • Section in Neurobiology, Yale University School of Medicine, New Haven, Connecticut 06510. DANIEL Y. TS'O • Department of Neurobiology, Rockefeller University, New York, New York 10021.

Cerebral Cortex, Volume 12, edited by Rockland *et al.* Plenum Press, New York, 1997.

ing of the modular organization within stripes, the functional properties of V2 stripes, the visual map with respect to the stripes, and the functional connectivity of V2 stripes with other cortical areas.

Early physiological exploration of the second visual area in the primate by Cowey (1964) showed that focal electrical stimulation of striate cortex resulted in responses in lateral prestriate cortex, the organization of which was topographically mirrored across the anterior border of primary visual cortex (V1). Subsequent studies, both anatomical and physiological (Zeki, 1969; Allman and Kaas, 1974; Gattass *et al.*, 1981), established V2 as a separate, topographically organized area. V2 occupies a long, narrow strip of cortex surrounding and anterior to V1, and in the macaque monkey, is located on the lip and in the depths of the lunate sulcus (see inset, Fig. 8). V2 is quite a large cortical area, second only to V1, and occupies roughly 10% of all neocortex in the macaque. Historically this prestriate area has been referred to as area 18. However, since area 18 as defined by Brodmann (1909) has been shown to include parts of several other visual areas, the term V2 should be used when referring to the topographically defined second visual area in the macaque monkey. In some other species (such as the owl monkey; Allman and Kaas, 1974), the terms V2 and area 18 are indeed equivalent.

Cytochrome Oxidase

A significant milestone in the study of V2 came with the development of cytochrome oxidase staining (Wong-Riley, 1979a; Horton and Hubel, 1981) as well as 2-deoxyglucose methods (Tootell *et al.*, 1983; Humphrey and Hendrickson, 1983). These metabolic labeling methods revealed exquisite and distinctive structures within V1 and V2. As seen in Fig. 1, cytochrome oxidase histology reveals a lattice of darkly stained patches in V1, termed blobs, separated by

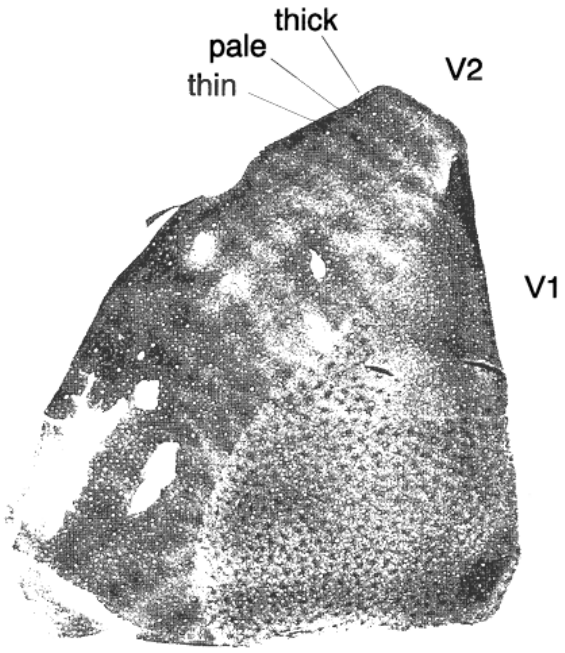

Figure 1. Cytochrome oxidase staining of V1 and V2. This tangential section of visual cortex in squirrel monkey reveals the lattice of darkly staining cytochrome oxidase blobs separated by lightly staining interblobs in V1 and the alternating cycle of thin/pale/thick/pale stripes in V2. The boundary between these two staining patterns is the V1/V2 border.

regions of lighter stain, termed interblobs (Livingston and Hubel, 1984). In contrast, V2 is characterized by a series of stripes extending orthogonally from the V1/V2 border. These stripes, which are alternatively dark *thin* and dark *thick* stripes separated by lightly staining *pale* stripes, cycle across V2 in thin/pale/thick/pale sequence. Relative to the cytochrome oxidase blobs in V1, V2 stripes are large (roughly 1–1.5 mm in width) and few in number (only 10–12 stripe cycles in dorsal V2). An accumulation of anatomical and physiological studies has lent support to the notion that the thin, pale, and thick stripes comprise functionally distinct compartments and are specialized for color, form, and disparity processing, respectively (DeYoe and Van Essen, 1985; Shipp and Zeki, 1985; Hubel and Livingstone, 1987; Ts'o *et al.,* 1990b).

Thin (color) stripes are not always thin; thick (disparity) stripes are not always thick. A word should be said about the equivalence of the stripes seen with cytochrome oxidase stain and the functionally defined stripes in V2. The nomenclature 'thin,' 'pale,' and 'thick' derives from descriptions of stripe patterns revealed by cytochrome oxidase staining. However, there remains a significant degree of variability in both the widths and the regularity of their pattern across V2, particularly in the macaque (Hubel and Livingstone, 1987; DeYoe *et al.,* 1990; Ts'o *et al.,* 1990b; Roe and Ts'o, 1995). There is substantial individual variation in the pattern of stripes and deviations from the strict cycle of thin/pale/thick/pale stripe structure. Furthermore, physiologically defined 'thin' stripes are not consistently narrower than 'thick' stripes as assessed by length of tangentially recorded sequences of receptive field types across stripes in V2 (Hubel and Livingstone, 1987; Zeki and Shipp, 1987; Roe and Ts'o, 1995). This observation calls into question the correlation between stripe width as seen in cytochrome oxidase staining and stripe width determined functionally. That is, the width of the physiologically defined color stripe often exceeds the width of the cytochrome oxidase thin stripe, and the width of the physiologically defined pale stripe is often narrower than the apparent width of the cytochrome oxidase pale stripe. Thus, it may be misleading to assume that the thick, pale, and thin stripes as defined histologically bear an absolute correspondence to the distribution of functional properties.

2. Receptive Field Properties with Respect to V2 Stripes

The distinctive striped functional organization in V2 is complemented by the emergence of new functional properties. The earliest studies describing the functional specialization of each of the three cytochrome oxidase stripe types, thick, thin, and pale, did not characterize the receptive field properties of cells found in each stripe with much detail. The descriptions were largely limited to noting the extent of orientation tuning, color selectivity, and binocular interaction (e.g., DeYoe and Van Essen, 1985). However, studies prior to the knowledge of the cytochrome oxidase stripes had already reported several receptive field types in V2 that indicated a further elaboration of receptive field properties beyond those observed in V1 (Hubel and Wiesel, 1970; Baizer *et al.,* 1977; Poggio and Fischer, 1977).

One of the first prominent differences noted between V1 and V2 is the lack of ocular segregation in V2, where most cells are binocularly driven (e.g., Hubel and Livingstone, 1987). In fact, for a population of the cells in V2 ocular information is combined in highly specific ways. As first reported by Hubel and Wiesel (1970), in their V2 recordings there was a high proportion of cells exquisitely sensitive to retinal disparity, which they called "depth cells" (Fig. 2). These retinal disparity cells (now also called tuned-excitatory obligatory binocular) only responded to simultaneous stimulation of both eyes with a very narrow range of disparities (e.g., 0.125–0.25 deg). Subsequent studies have localized these and other disparity cells primarily to the V2 thick stripes (DeYoe and Van Essen, 1985; Hubel and Livingstone, 1987; Ts'o *et al.*, 1990b; Roe and Ts'o, 1995). One of the important transformations in the representation of disparity information from V1 to V2 is the establishment of a definitive functional organization for disparity in V2. Not only are the disparity cells concentrated within the thick stripes, but within the thick stripes there is a clustering of disparity cell types, with tuned excitatory, tuned inhibitory, and near and far (crossed and uncrossed) disparity cells (Poggio and Fischer, 1977; LeVay and Voigt, 1988) each segregated into their own set of patches within a single thick stripe (Ts'o *et al.*, 1990b). Although the thick stripes have also been cited as the compartment for motion processing in V2, most studies have not reported a particularly high concentration of directionally selective cells anywhere within V2 (Livingstone and Hubel, 1987; Ts'o *et al.*, 1990b; Peterhans and von der Heydt, 1993; Levitt *et al.*, 1994a). Thus the mainstream motion pathway may bypass V2 and enter V5 (MT) directly from V1.

In the color domain, the receptive field types that have been reported include several that have also been described in V1: type I (single color opponent center surround), type II (center-only color opponent), modified type II (center color opponent with broadband suppressive surround), and color oriented (Ts'o and Gilbert, 1988). One marked distinction of these V2 color cells in comparison

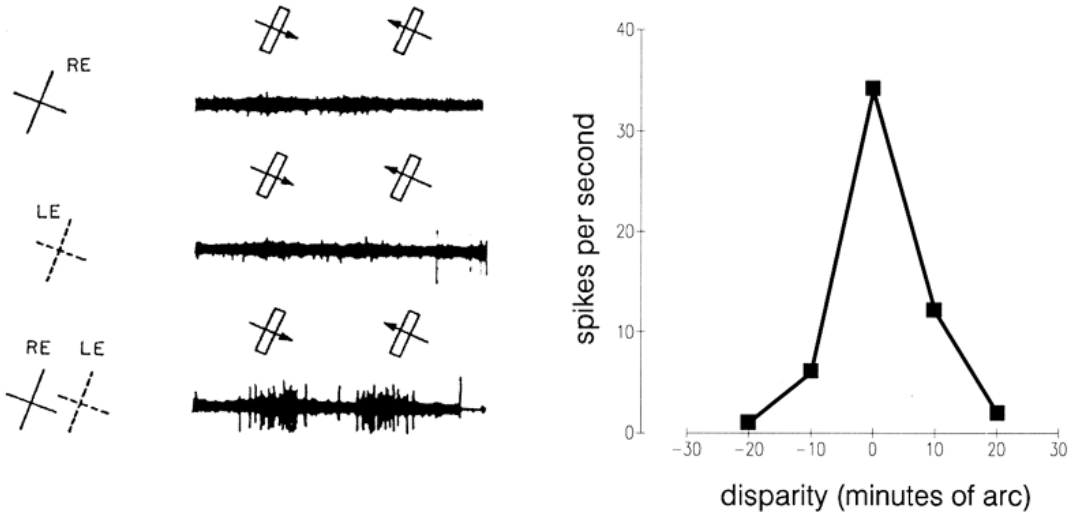

Figure 2. Disparity cell. An obligatory binocular cell recorded in a thick stripe in V2. It is not responsive to monocular stimulation, neither left eye nor right eye alone, but responds robustly to binocular stimulation (left bottom) within a very narrow range of retinal disparities (right). After Hubel and Wiesel (1970).

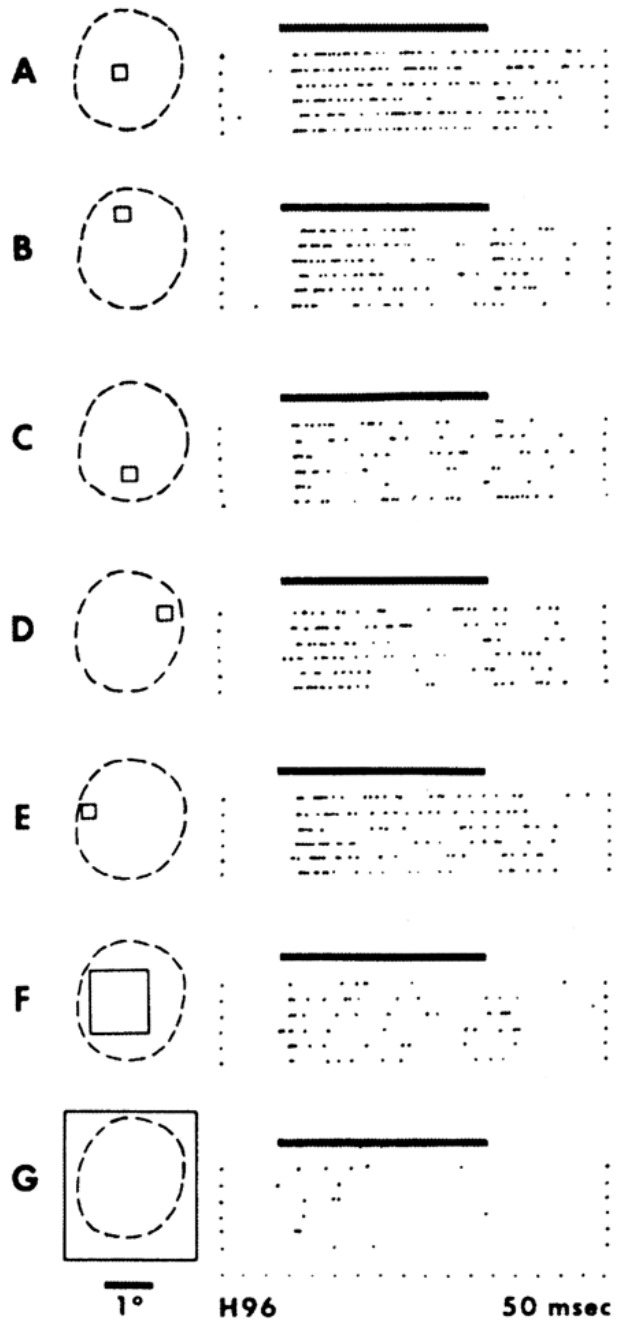

Figure 3. Spot cell. Responses of a spot cell to stimuli at different positions and of different sizes. Responses (raster plots on right) are robust to small (much smaller than receptive field size) spots of light within the receptive field (A–E). Larger spots tend to reduce the response (F) and illumination of the entire receptive field virtually silences the cell (G). From Baizer *et al.* (1977).

to their V1 counterparts is that they exhibit no eye preference, but instead, like most V2 nondisparity cells, are completely binocular. In addition to these color cells, a new type of color receptive field has been described, the spot cell or complex unoriented cell (Bazier *et al.*, 1977; Hubel and Livingstone, 1985, 1987; Roe and Ts'o, 1995). The spot cell may be understood as a modified type II cell that has "complexified" and has a degree of position invariance in the center response. It responds well to a small spot of light of a particular color that is positioned somewhere within its receptive field, which may be 10 times or more larger than the optimal spot size (Fig. 3). Another transformation in color responses that is apparent when comparing V2 with V1 color cells is that the range

of color preferences is much greater in V2, suggesting that there is considerable mixing of the two color opponent systems, red/green and blue/yellow, in or prior to V2 (Ts'o *et al.*, 1990b).

In V2 there is a greater proportion of color oriented cells (Ts'o and Gilbert, 1988; Ts'o *et al.*, 1990b) in comparison to V1, and they are often found at the borders between the thin and pale stripes. Among the population of color oriented cells in V2, a particularly interesting type, the "color border" cell, has been described (Ts'o *et al.*, 1990b). This new type of color oriented cell is somewhat analogous to the double color opponent cell in that its optimal stimulus is an oriented color edge with one color (e.g., red) on one side and a different color (e.g., green) on the other. It is then an appropriate cell type for detecting borders or contours defined by color contrast. Another novel class of color oriented cell found in V2 is the color disparity cell (Ts'o *et al.*, 1991, 1995). These cells are found at the borders between color and disparity regions, and exhibit both color and disparity tuning. The mixing of the submodalities of color and orientation and of color and disparity is also indicated in the pattern of anatomical connections (Ts'o *et al.*, 1991; Levitt *et al.*, 1994b; Malach *et al.*, 1994), and represents interactions between the otherwise segregated processing of form, color, and disparity information. Such cross-modal interactions may aid in the maintenance of the registration of the separate maps and computations of the form, color, and disparity systems and thus contribute to a unified visual percept.

In the form domain, it has been reported that a substantial portion of V2 oriented cells, particularly in the pale stripes, exhibit end-inhibition. A further elaboration of this property has been described by von der Heydt and Peterhans (1989; Peterhans and von der Heydt, 1989) in which a class of oriented cells, in addition to responding to true contours, also respond to illusory contours (also termed subjective contours or anomalous contours, see Fig. 4). These investigators suggested a model for illusory contour cells built from input provided by end-inhibited cells. Motion coherence cells have also been described which respond to a coherently moving group of dots. While their responses to single dots are unoriented, a colinear array of dots yields an oriented response which matches the orientation selectivity of the cell to a luminance contrast border. These illusory contour cells have been found primarily in the thick and pale stripes (Peterhans and von der Heydt, 1993).

A controversy that began with several physiological studies exploring the degree of functional segregation between the blobs and interblobs of V1 has raised similar questions in V2. In V1 it has been reported that color and orientation information is largely segregated, with the blobs primarily containing unoriented monocular color cells and the interblobs primarily oriented noncolor-selective cells (Livingstone and Hubel, 1984; Tootell *et al.*, 1988b; Ts'o and Gilbert, 1988). However, some investigators, using somewhat different methods, report little or nor segregation or specialization for color in the blobs (Lennie *et al.*, 1990; Leventhal *et al.*, 1995). A similar, but lesser discrepancy exists for the issue of whether the V2 thin stripes are specialized for color processing, and whether there is substantial functional segregation in the stripes overall (Levitt *et al.*, 1994a). The approaches the various studies have taken in examining the

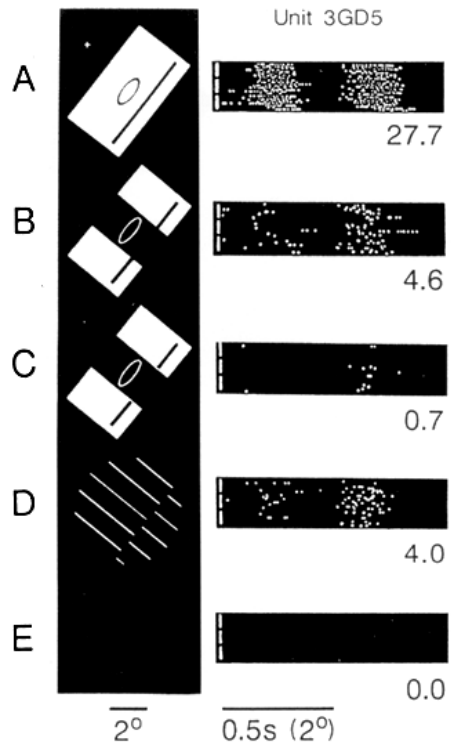

Figure 4. Illusory contour cell recorded in V2 of an alert monkey. This cell (response field indicated by ellipse) responds robustly (raster plots on right) to an oriented dark bar moving on a light background (A). Its responses to similarly oriented illusory contours are also quite strong (B, D). However, with the closing lines the illusory-bar response is virtually abolished (C). From Peterhans and von der Heydt (1989).

color properties of blob and interblob cells differ greatly, particularly in the means for generating color stimuli, but also in localizing the recording site. It seems clear that the extent of functional segregation in V2 is much more apparent when considering the distribution of some functional properties, such as color and disparity, as opposed to others, such as spatial and temporal frequency tuning. Results from functional imaging and 2-deoxyglucose studies do indicate that the blobs of V1 and the thin stripes of V2 are selectively activated with color stimuli and in general confirm the notion of functional segregation within the stripes of V2 (Tootell and Hamilton, 1989; Ts'o *et al.*, 1990b, Malach *et al.*, 1994). Nevertheless more detailed corroboration between functional anatomical methods and electrophysiology will be necessary to fully resolve these issues.

In summary, although our understanding of the range of receptive field properties of V2 cells must be regarded as preliminary, it is clear that in each of the color, form, and disparity domains significant functional transformations are performed. While V1 is characterized by cells concerned with ocularity, orientation of contrast borders, and unoriented color properties, one observes in V2 the emergence of a distinctive organization for binocular disparity, and of cells signalling perceptual contours, complex color properties, and interactions between color/form and color/disparity information. These properties are summarized in Fig. 5. It is apparent that one common theme in V2 and beyond (e.g., V4, MT, MST) is the convergence of inputs to generate higher order receptive field properties (such as spot cells or illusory contour cells) that integrate information across increasing spatial extents (Hubel and Livingstone, 1985; Peterhans and von der Heydt, 1993). However, much of the relationship between specific cells types and higher order visual perceptions needs to be further investigated (Merigan *et al.*, 1993).

Figure 5. Summary of schematics of receptive field types found in V2. The top row depicts cell types that are also found in V1, while the bottom row shows cell types that are either particularly notable in V2 or described only in V2. Certain other cell types, such as directional cells, have been omitted for the sake of brevity.

3. Modular Organization within Stripes

A further examination of the architecture of the V2 stripes has revealed an additional level of substructure and modularity within single stripes. Histologically, cytochrome oxidase stains of the V2 stripes often have an uneven, mottly appearance. The earliest evidence of subcompartments within V2 stripes came from anatomical studies examining the pattern of corticocortical connections between V1 and V2 (Rockland and Pandya, 1979; Wong-Riley, 1979b; Weller and Kaas, 1983). In these experiments, injections of anterograde tracers into V1 resulted in clusters of terminal label in V2 measuring roughly 400 μm in diameter (Wong-Riley, 1979b). These clustered connections from V1 are likely to arise from single axons terminating in V2 in clusters 200 μm in size and separated by 200–500 μm in layers 4 and lower 3 (Rockland and Virga, 1990). Patchy patterns of connectivity have also been observed with other areas, such as V4 (DeYoe *et al.*, 1994), MT (Shipp and Zeki, 1989; Krubitzer and Kaas, 1989; DeYoe *et al.*, 1990), and the pulvinar (Ogren and Hendrickson, 1977; Curcio and

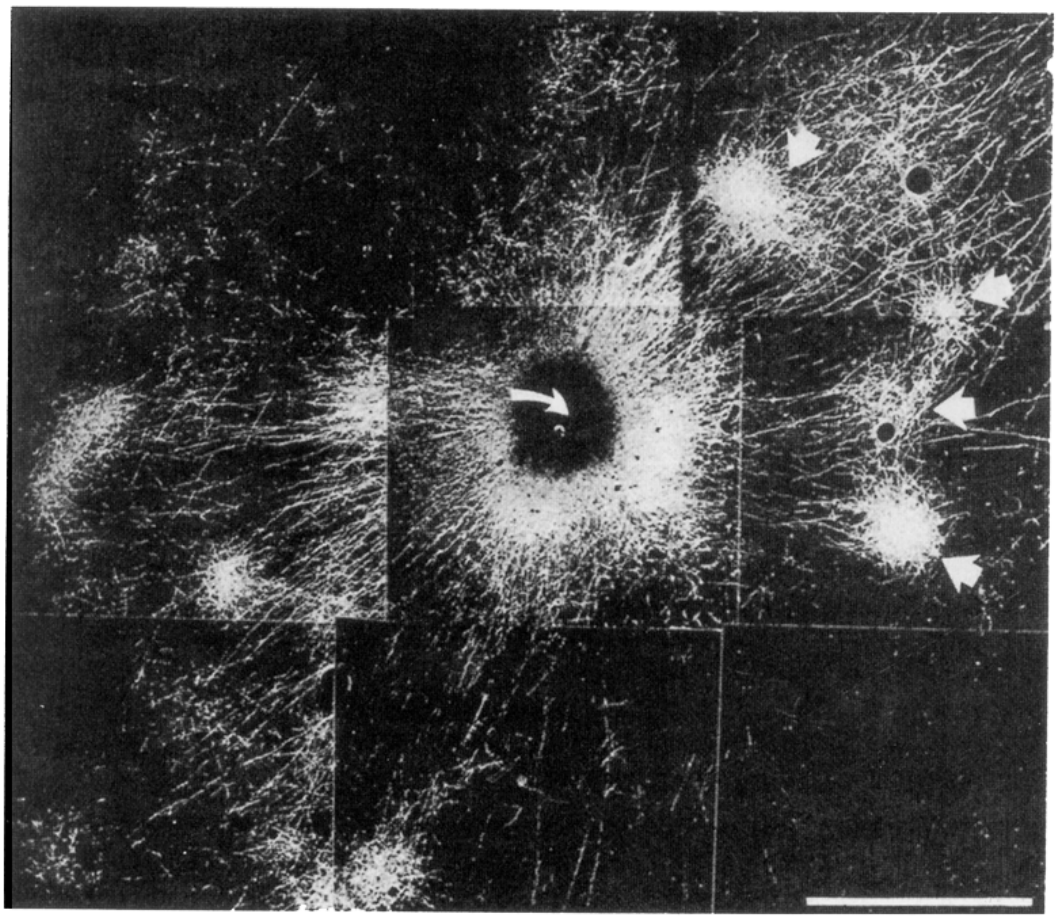

Figure 6. Intrinsic horizontal connections in area V2. This is a dark-field, low-power montage of a tangential section from V2 that has been flattened. Transported label from a biocytin injection (curved arrow) reveals a network of radiating fibers and clustering into patches (large arrows) farther away. Scale bar = 1 mm. From Malach *et al.* (1994).

Harting, 1978; Horton, 1984; Levitt *et al.,* 1995), as well as from intrinsic connections in V2 (Rockland, 1985; Amir *et al.,* 1993; Levitt *et al.,* 1994b; Malach *et al.,* 1994) (Fig. 6). These findings strongly suggest anatomical and therefore physiological subcompartments within single V2 stripes.

2-Deoxyglucose (Tootell and Hamilton, 1989), optical imaging (Malach *et al.,* 1994; Ts'o *et al.,* 1990b, 1991, 1995), and electrophysiological (Ts'o *et al.,* 1990b, 1991; Roe and Ts'o, 1995) methods have gone on to demonstrate a functional modularity within single V2 stripes that is likely to correspond to the stripe subcompartments revealed anatomically. Optical imaging reveals functionally uniform domains, about 0.4–0.5 mm in diameter, in each of the three stripe types. These domains contain clusters of cells with similar receptive field properties. For example, in thin stripes, there are subcompartments dedicated to the representation of color versus luminance response properties (Fig. 7). Disparity stripes have been shown to be characterized by clusters of near, far, tuned-excitatory, or tuned-inhibitory cells (Ts'o *et al.,* 1991). Orientation subcompartments in V2, prominent in pale stripes and disparity stripes, contain cells sharing

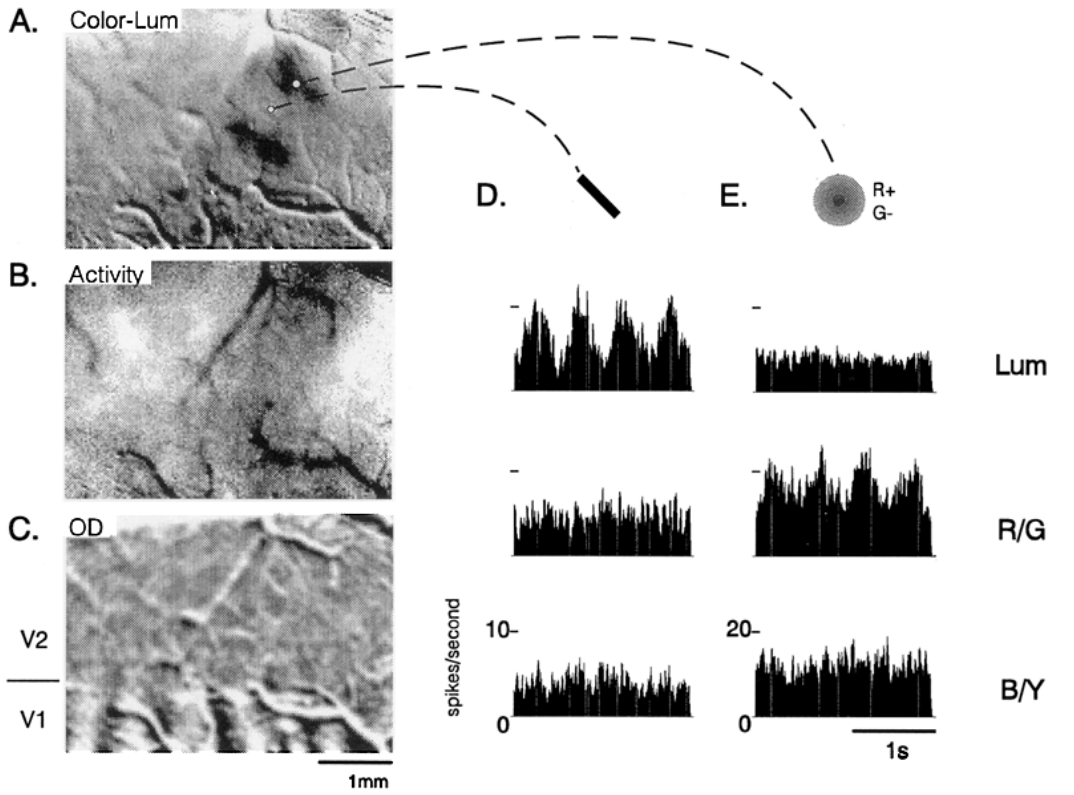

Figure 7. Optical imaging and single-unit electrophysiology in subcompartments of a single V2 color stripe. On the left, three images taken of the same region of V2, under three different imaging paradigms, designed to reveal the ocular dominance columns of V1 (C), the stripes of V2 (B), and regions that prefer color over luminance stimuli (A). When imaging for color versus luminance (A), the single V2 thin stripe can be seen to be actually composed of several distinct modules or subcompartments. On the right, single-unit recording confirms that light subcompartments prefer low-spatial-frequency (1 cyc/deg) luminance gratings (D). Dark subcompartments prefer color isoluminant red/green (R/G) gratings (E); this particular cell was qualitatively described as red-ON, green-OFF type II and did not respond to modulations in the blue/yellow (B/Y) direction in color space. From Ts'o *et al.* (1997).

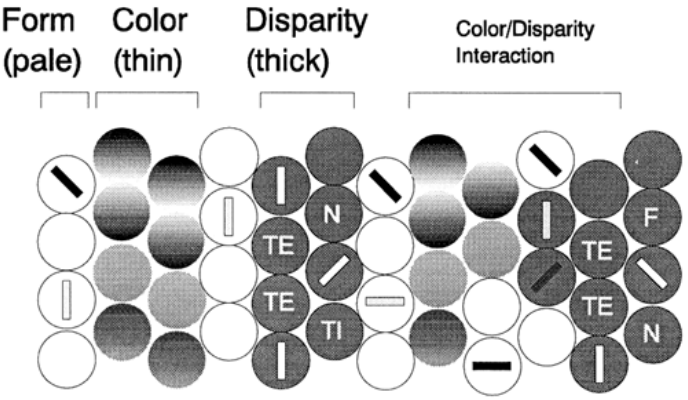

Figure 8. Schematic model of modular organization within V2. Within thin stripes, different color subcompartments process information along different axes in color space. Pale stripes contain orientation-selective subcompartments, some of which are also color-selective. Within disparity stripes are subcompartments containing either near cells, far cells, tuned excitatory cells, or tuned inhibitory cells. At mergings between thin and thick stripes, clusters of color disparity cells are observed.

a single preferred orientation and are adjacent to other orientation subcompartments of quite different orientation selectivity, unlike the smoothly changing orientation representation within V1 (Ts'o *et al.,* 1990b). Such anatomical, functional, and topographic (see Section 4) evidence suggests that these modules may constitute the fundamental units of representation in V2 (Ts'o *et al.,* 1997). Thus, each stripe within V2 may be seen as a collection of $^1/_2$-mm-sized modules, each of which is dedicated to processing a specific submodality within either the color, form, or disparity domain (Fig. 8).

In describing the V2 stripe subcompartments, roughly conserved in size regardless of whether they subserve color, orientation, or disparity processing, it is interesting to note the parallel to the blob/interblob compartments of V1. The blobs of V1, though they apparently subserve color and brightness processing, are roughly the same size as a single orientation column in the interblobs of V1. These observations lead to the idea that in each cortical area, there is a characteristic functional module size, roughly independent of the particular functional specificity. As the blobs and orientation columns of V1 occupy about one-quarter the cortical surface area of a V2 stripe subcompartment, we note that the characteristic module size increases from V1 to V2. Anatomical and physiological studies of V4 (Amir *et al.,* 1993; DeYoe *et al.,* 1994; Ghose *et al.,* 1997; Ts'o *et al.,* 1997) suggest that similar, but even larger, stereotyped functional modules also exist in V4. Thus, although when one considers the V2 stripes as a whole, it appears that the functional organization of V2 is quite different from that of V1, greater similarity may be found by comparing the blob/orientation modules of V1 to the subcompartments of the V2 stripes.

4. Topography

The traditional physiological method of sensory cortical mapping has been to make a gridlike map with multiple vertical penetrations throughout a cortical area. This method is well suited to sampling extensively over an entire cortical area, including regions which are buried in cortical convolutions. This approach has been commonly used in mapping the visual field representation in V1 of

macaque monkeys (Talbot and Marshall, 1941; Daniel and Whitteridge, 1961; Dow *et al.*, 1981), vervet monkeys (Guld and Bertulis, 1976), owl monkeys (Allman and Kaas, 1971), and squirrel monkeys (Cowey, 1964). With similar methods, area V2 has been mapped in the owl monkey (Allman and Kaas, 1974; Sereno *et al.*, 1994, 1995), the squirrel monkey (Cowey, 1964), the cebus monkey (Rosa *et al.*, 1988), and the macaque monkey (Van Essen and Zeki, 1978; Gattass *et al.*, 1981). Area V2 in the macaque is a quite convoluted structure, covering roughly 1000^2 μm, with both dorsal and ventral territories, little of which is exposed for easy areal mapping. Despite these difficulties, Gattass *et al.* (1981) were able to reconstruct the visual map from vertical penetrations which passed through buried convolutions. Figure 9 (which is based on Gattass *et al.*, 1981) illustrates the basic visuotopic mapping in V2. Inferior visual fields are repre-

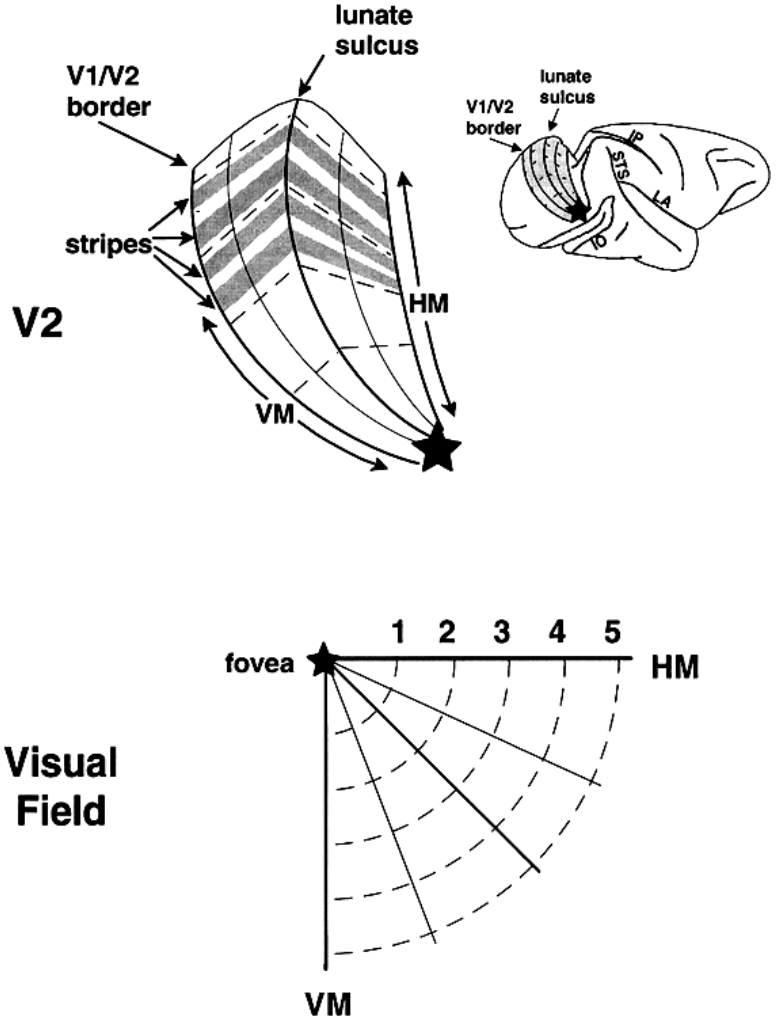

Figure 9. Schematic of visual representation in dorsal V2. Area V2 is located on the caudal bank of the lunate sulcus and extends onto the operculum in the macaque brain (shaded region in upper left inset). An expanded view of this region (above) illustrates the representation of the visual field (below) in V2. Representation of the vertical meridian (VM) lies on the V1/V2 border and that of the horizontal meridian (HM) lies in the depths of the lunate sulcus. Lines of isoeccentricity (dashed lines) run perpendicular to the V1/V2 border. Lines of isopolarity (solid lines) run roughly parallel to the V1/V2 border and converge at the foveal representation (star), which is located laterally on the brain surface. The orientation of stripes in V2 is indicated (gray stripes).

sented dorsally and superior fields ventrally. Area V2 is bounded posteriorly by the vertical meridian representation (VM), located at the V1/V2 border, and anteriorly by the horizontal meridian representation (HM), located in the depths of the lunate sulcus. Thus, isopolar representations (solid lines) run roughly parallel to the VM and HM, while isoeccentricity is represented in the anterior–posterior direction (dashed lines). Since this type of mapping results in a split horizontal meridian representation (one in dorsal V2 and one in ventral V2), it has been termed a "second-order transformation" (Allman and Kaas, 1974). In fact, there appears to be an overrepresentation of a few degrees above and below the horizontal meridian; receptive fields at the anterior border of dorsal V2 extend above the HM and those at the anterior border in ventral V2 extend below the HM (Gattass *et al.*, 1981).

One of the most definitive criteria for the delineation of cortical areas has been that of a single topographic representation. Within an area, representations are usually continuous, as evidenced by gradually shifting receptive field locations. Boundaries between areas are often marked by reversals or discontinuities in topography, changes in receptive field properties, changes in receptive field scatter (a measure of the orderliness of receptive field progression), and changes in cortical magnification. However, the functional specializations in visual cortex, particularly in V2 with its dozen or so millimeter-sized stripes, have prompted a reexamination of these topographic principles.

4.1. Multiple Maps

The division of V2 into functionally distinct stripes raised new questions with respect to topography. In V2, since stripes are oriented anteroposteriorly (Fig. 9, gray stripes), isoeccentricity lines map parallel to the stripes, and lines of isopolarity map across the stripes. How do each of the three stripe types provide sufficient coverage of the visual world within their respective modalities?

Recent studies (Zeki and Shipp, 1987; Zeki, 1990; Roe and Ts'o, 1995a) have shown that the visual map in V2 actually consists of three distinct, interleaved maps. By using optical imaging (Grinvald *et al.*, 1986, 1988; Frostig *et al.*, 1990; Ts'o *et al.*, 1990a) to determine the location of stripes and stripe borders *in vivo*, Roe and Ts'o investigated the topography of V2 with respect to these functionally identified stripes with long, tangential electrode penetrations which densely sampled each stripe and which crossed all stripes within a thin/pale/thick/pale stripe cycle (Fig. 10). These studies found that each region of visual space is represented three times, once by color nonoriented cells in the thin stripes, once by broadband oriented cells in pale stripes, and once by disparity-selective cells in the thick stripes. Receptive field progressions within stripes were accompanied by discontinuities or "jumps back" in progression at stripe borders. For example, thin/pale stripe sequences contain progressions of nonoriented color cells followed by a jump back in receptive field position at the thin/pale border followed by a progression of oriented broadband cells (Fig. 11). Each progression within a stripe is slightly shifted relative to that in the previous stripe. In addition, to avoid any holes or gaps in topographic representation within any single functional submodality, continuity in coverage is achieved from one stripe to the next like stripe (e.g., from thin stripe to thin stripe). Thus,

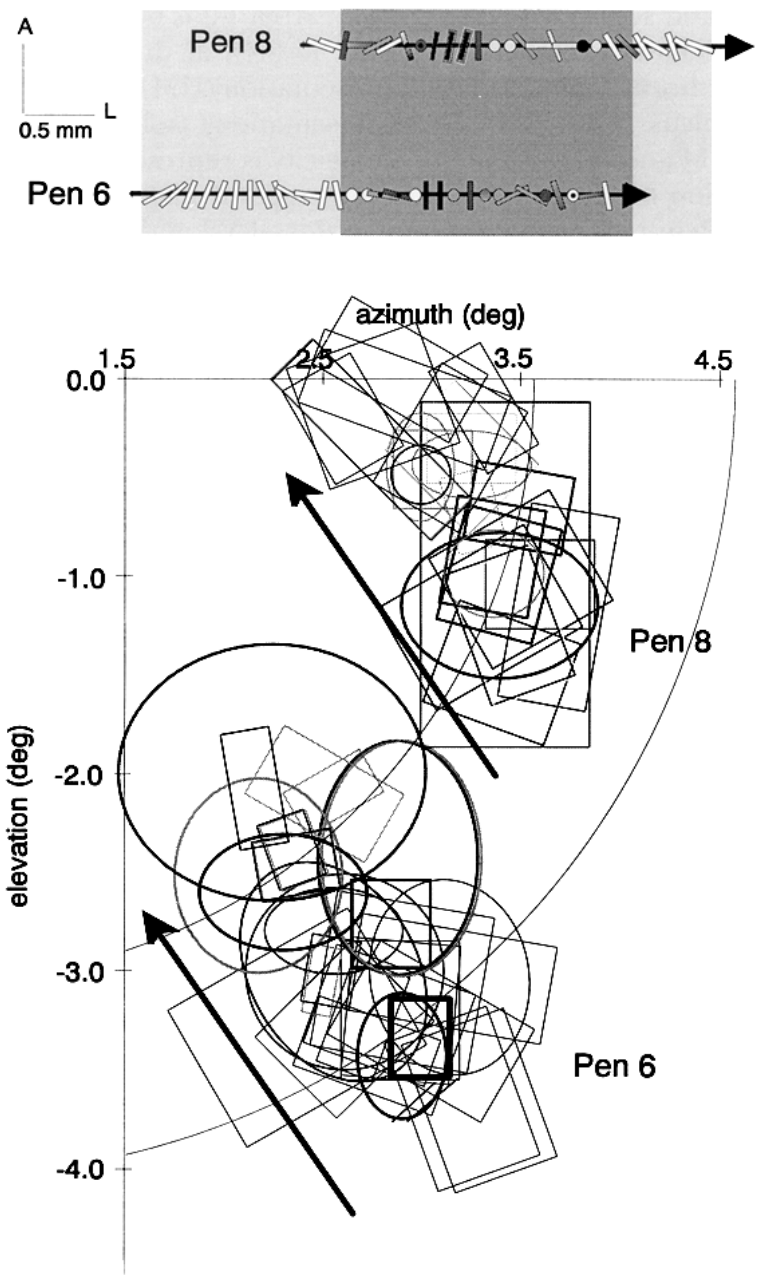

Figure 10. Parallel tangential penetrations oriented across stripes record parallel receptive field progressions. These progressions cross lines of isoeccentricity (two arcs shown). Above: Illustrated at the top are the receptive field types recorded along two penetrations (Pen 6 and Pen 8) and the positions of these recording sites with respect to the color stripe (dark gray) and pale (light gray) stripes (A, anterior; L, lateral), as determined by optical imaging. Broadband oriented cells are indicated by white bars; color nonoriented and oriented cells by light and dark gray circles and bars, respectively; and disparity cells by black bars (color-selective disparity cells are indicated with outlines). Symbols with mixed grays indicate those color cells responsive to either red and green or blue and yellow wavelengths. Spot cells are indicated by symbols with black dots. Below: Receptive field plots of cells shown above. Receptive fields of broadband cells are drawn in black outline and color cells in dotted outline. Rectangles and circles/ovals indicate oriented and nonoriented receptive fields, respectively. Disparity cells are coded with bold lines. Large arrows indicate direction of overall receptive field progression recorded in each penetration.

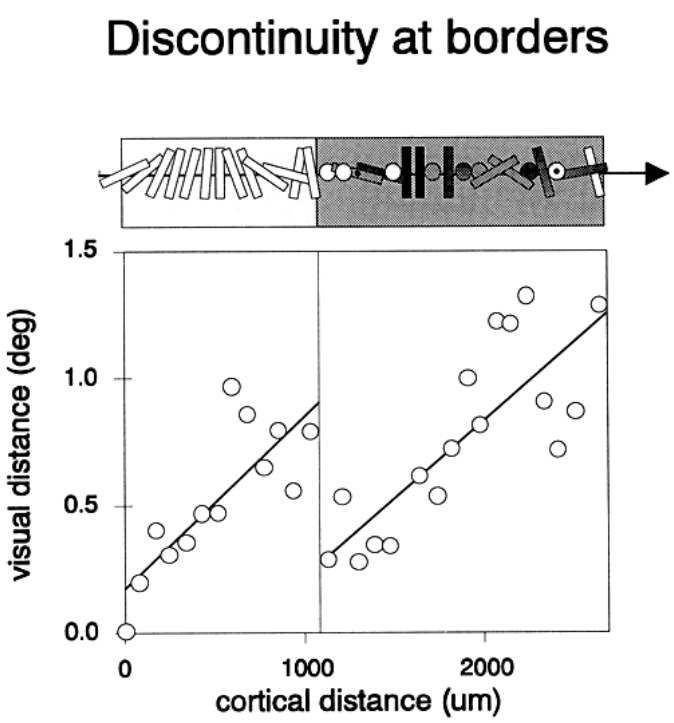

Figure 11. Discontinuity or jumps back in receptive field progression at stripe borders. Top: Same as Fig. 10, Pen 6. Bottom: abscissa: position along tangential electrode penetration that receptive fields were recorded; ordinate: size of receptive field shift from first receptive field recorded in penetration. Points are fit by linear regression. The data suggest the presence of two progressions separated by a discontinuity at the pale/color stripe border.

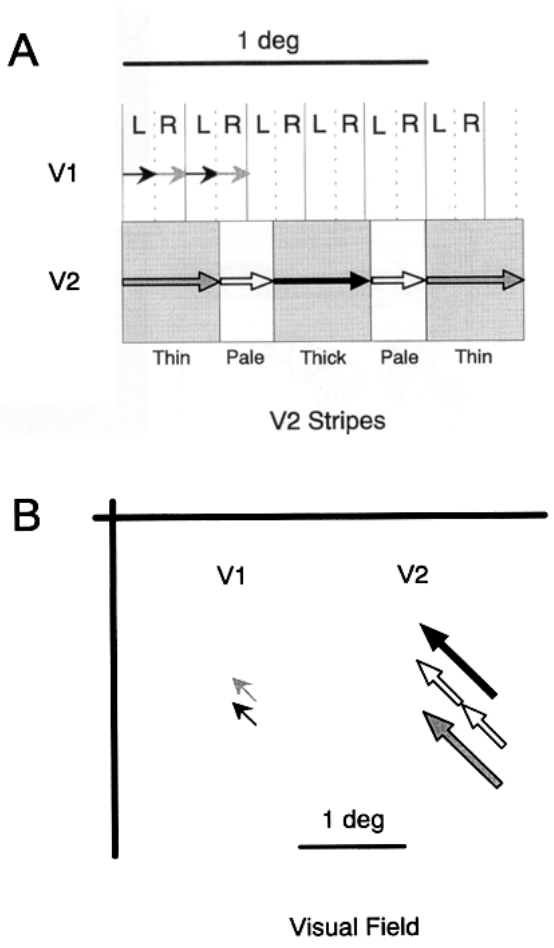

Figure 12. Summary of interleaved "one step forward, two steps back" mapping schemes in both V1 and V2. In V1, ocular dominance is doubly represented. In V2, color, form, and disparity are separately represented, resulting in three interleaved maps.

representation in multiple domains, discontinuity at stripe borders, and continuity between like stripes are characteristic of the visual map in V2.

This discontinuous and interleaved strategy is very similar to that described by Hubel *et al.* (1974) in V1 with respect to representation by the left and right eyes (Hubel and Wiesel, 1977; Blasdel and Fitzpatrick, 1984). In V1, Hubel and Wiesel (1977) had described a "two steps forward, one step back" progression of receptive fields recorded in tangential penetrations through layer 4C of V1 across ocular dominance columns. That is, each locus in visual space is represented twice in succession, once by the right eye and once by the left, accompanied by a slight shift in overall progression between the two eyes (Fig. 12A). The visual world is thus represented twice in V1, once by each eye. In a manner similar to that taken in V1, receptive fields in V2 progress in a "two steps forward, one step back" fashion from stripe to stripe, albeit with much larger steps (roughly four times as large) (Fig. 12B). These data suggest that V2 sees three different versions of the world, one in color (thin stripes), one in form (pale stripes), and one in depth (thick stripes). In a sense, V2 takes these three views, slices each one into stripes, and them interleaves them. This idea is illustrated in Fig. 13.

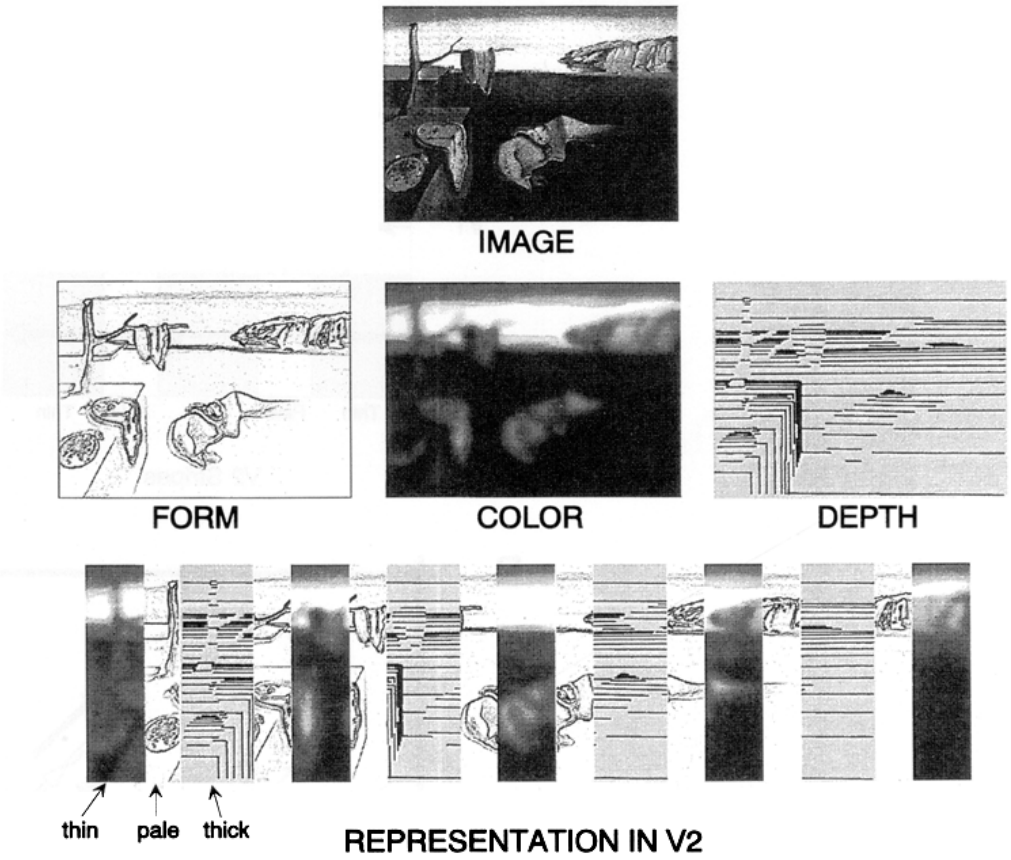

Figure 13. How V2 sees the world. Top: Original image: *Persistence of Memory* by Salvadore Dali. Middle: Decomposition into three images, each defined by either color, form, or depth information. Bottom: Interleaving of these three views in V2. Note the resulting relationships of objects when multiply represented in the different stripe compartments.

4.2. Cortical Magnification, Anisotropy, Modular Maps, and Receptive Field Size

The term cortical magnification was originally coined by Daniel and Whitteridge (1961) to refer to the amount of cortex (in linear distance) devoted to representing each degree of visual space. In V1, this quantity varies (roughly) inversely as a function of eccentricity; greater cortical area is occupied by central fields and less by peripheral visual field representation. While linear magnification is related to a particular axis in cortex, areal magnification is calculated from total area of cortex representing a particular locus in space. Thus, it is possible for two different cortical areas to have similar areal magnification factors for a particular eccentricity, but different component linear magnification factors.

4.2.1. Anisotropy

In comparing cortical magnifications between V1 and V2, it is important to take into account the two axes of representation. V1 contains an inherent anisotropy due to the rerepresentation between the two eyes; the cortical magnification in the axis across ocular dominance columns is roughly twice that along ocular dominance columns (Sakitt, 1982; Tootell *et al.*, 1983, 1988a; Grinvald *et al.*, 1994; Roe and Ts'o, 1994; cf. Malach *et al.*, 1993). As would be predicted by the reflection of the visual field across the V1/V2 border, in the axis parallel to the border (that is, *across* stripes in V2), overall cortical magnification is similar to that in V1. However, in the axis parallel to the stripes in V2, the magnification is much lower, leading to significant anisotropy in the map (Roe and Ts'o, 1995a; cf. Rosa *et al.*, 1988). The cortical dimensions of area V2 (including both dorsal and ventral V2) are at least 5–7 times greater in extent across the stripes than along them (personal observations; cf. Tootell *et al.*, 1983; Van Essen and Maunsell, 1983). If anisotropy in V2 were due solely to the triple representation of the visual map, then the cortical magnification *across* the stripes should simply be three times that *along the stripes*. Each of the three maps taken individually would then be isotropic. However, recent evidence suggests that there is a 2:1 (across:along) anisotropy *within single stripes*, resulting in an overall 6:1 anistropy in V2, a ratio consistent with the anatomical dimensions of V2 (Roe and Ts'o, 1995).

4.2.2. Cortical Magnification in Stripes

At visual eccentricities of 2–5 deg, the cortical magnification factors *across* stripes are roughly 1.3 mm/deg *for each of the three stripe systems* (Roe and Ts'o, 1995). That is, at this eccentricity a full cycle of representation would cover on average roughly 4 mm (= 1.3 + 1.3 + 1.3 mm) of cortex per degree of visual representation. This overall magnification factor in V2 approximates those reported in the 2- to 5-deg eccentricity of V1 (approximately 2–5 mm/deg) (Daniel and Whitteridge, 1961; Hubel and Wiesel, 1974; Dow *et al.*, 1981; Van Essen *et al.*, 1984). Since there are twice as many pale as color or disparity stripes, one might have expected cortical magnification in pale stripes to be somewhat high-

er. However, that is not the case: cortical magnification in pale stripes is not significantly different from that in color stripes. Coupled with the fact that color stripes are on average twice the width of pale stripes (as indicated by the length of recording sequences in each stripe), this argues that the amount of cortex devoted to broadband orientation representation is similar to that of color representation. In other words, on average, color and disparity stripes are twice as wide as pale stripes.

4.2.3. Modular Maps

Anisotropy within V2 stripes may be directly related to the modular organization within stripes. As we have seen, anisotropy can arise from duplicating the map in one axis of visual field representation. Such remapping also occurs within single stripes, resulting in a cortical magnification factor across the stripe which is twice that along the stripe. Two remapping strategies within stripes have been observed. The first is quite similar to that of the "two steps forward, one step back" described in V1. The second way in which anisotropy within stripes may be created results from larger receptive field scatter in one axis relative to another. Some color stripes resort to large receptive field size and scatter to achieve coverage by each modular domain. Another indication that color, pale, and disparity stripes in V2 may have different coverage strategies derives from the fact that receptive field sizes and scatter in color stripes are generally greater than those in either pale or disparity stripes. Thus, a single cortical area may take advantage of a combination of different mapping strategies to achieve coverage. At a global level coverage is achieved by rerepresentation across the stripes; at a more local level both rerepresentation and large receptive field size and scatter are called upon to provide coverage.

4.2.4. Relative Receptive Field Size and Scatter in Different Stripes

There is greater receptive field size and scatter for the color stripes than for the disparity and pale stripes (Roe and Ts'o, 1995). Although the exact relationship between these findings to psychophysical measures of color, form, and depth perception has not been explored, it is reasonable that the color system would require a less precise mapping than either the form or depth system. The visual system's ability to localize accurately isoluminant color borders is far less precise than its ability to localize luminance edges or disparity boundaries (cf. Morgan and Aiba, 1985). Unoriented color information may serve to fill in the regions bounded by luminance or disparity contours and therefore would require less positional precision.

4.3. Point Image versus Point Set

The extent of the receptive field of a cell reflects the region of visual space which, when appropriately stimulated, causes the cell to respond. The size of an aggregate receptive field, defined as the size of visual space covered by the receptive fields of all cells within a column of cortex, reflects the minimal amount of visual space that a single column of cortex "sees." The term *point*

image refers to the amount of cortex activated by a point stimulus in space and is calculated as the product of cortical magnification and local scatter.

Receptive field size in V2 (defined as the square root of receptive field area) is roughly 2–3 times that in V1 at corresponding eccentricities (see Gattass *et al.*, 1981, Fig. 13). Figure 13 illustrates the typical scatter recorded in single vertical penetrations in a pale stripe and a color stripe at any eccentricity of 2–5 deg. While there is some suggestion of anisotropy within the scatter, it is not sufficient to account for the 2:1 anisotropy within single V2 stripes.

The point image in V2 is somewhat different than that in V1. We find it useful to introduce a term distinct from point image, which we refer to as *point set*. Whereas point image refers to the amount of cortex which represents a point in space "by a comfortable margin" (Hubel and Wiesel, 1974), point set refers to the smallest fundamental unit which contains all relevant stimulus dimensions. In V1, the point image is roughly a 2 mm × 2 mm block of cortex which contains two sets of ocular dominance columns. Point set then refers to the 1 mm × 1 mm unit which contains a single ocular dominance hypercolumn, orientation hypercolumn, and possibly a single color hypercolumn (cf. Landisman *et al.*, 1994). In V2, it is likely that the color hypercolumn, the orientation hypercolumn, and the disparity hypercolumn is each contained within a single thin, pale, and thick stripe, respectively. Thus, a point set in V2 would be equivalent to the territory within one stripe cycle. However, the hypercolumn in each visual modality in V2 resides in nonoverlapping cortical territory, unlike the orientation and ocular dominance hypercolumns of V1. The size of this minimal unit of representation is roughly four times greater in extent in V2 than in V1 (4 mm vs. 1 mm in extent). Optical imaging experiments using small point stimuli (0.1–0.5 deg in size) have directly shown a full stripe cycle of activation and two or three stripe cycles of secondary activation, likely due to lateral or divergent activation. Thus, point image in V2 is a significantly larger construct and spans at least two stripe cycles (Roe and Ts'o, 1994). This suggests a V1/V2 divergence ratio of at least two and perhaps as much as six in the cortical axis across stripes. Furthermore, in contrast to the point image in V1, in V2 the point images in the color domain, the orientation domain, and the disparity domain are represented separately in different pieces of cortical tissue.

4.4. What Makes V2 a Single Cortical Area?

The criterion of a single topographic map has traditionally been a strong basis for defining a cortical area. However, the finding of multiple visual representations within V2 reintroduces the issue of what it is that defines a cortical area. The anisotropic cortical magnification within V2 is consistent with the presence of at least three, and perhaps six, different representations, interleaved among and perhaps within the V2 stripes. Each stripe also contains its own characteristic receptive field sizes. The point images in each of the color, form, and disparity domains span distinct pieces of cortical tissue within V2. Given this architecture, one could view each stripe system as a complete and independent representation. What then qualifies V2 as a single cortical area, rather than three areas?

Although these multiple, discontinuous representations exist in V2, since

they are roughly in register when considering an entire stripe set, a more macroscopic description of V2 would find a single topographic map, albeit with local distortions and discontinuities. Several other considerations help justify the view that V2 is indeed a single visual area. Although V2 contains segregated multiple functional representations, we would suggest that each submodality within V2 performs a similar and characteristic functional transformation on its particular inputs. These stereotyped transformations, we speculate, are implemented with similar circuits residing within or associated with the fundamental V2 module and construct higher order receptive field properties, regardless of the type of visual input. Thus, these common transformations shared by modules of different modalities within V2 are another justification for characterizing V2 as a single cortical area. A second important component in unifying the three stripes in V2 is the network of intrinsic connections known to link stripes of different modalities. These intracortical connections may form the mechanism by which close coordination of different submodalities is achieved, perhaps for the purpose of binding multiple views into one. Thick, pale, and thin stripes would then behave not as completely independent domains, but rather as a coordinated whole. Thus we suggest that the overall topography of V2, its stereotyped functional transformations, and the interactive relationships between the otherwise segregated stripe compartments are all justifications for characterizing V2 as a single cortical area.

5. Connectivity

We now turn to the patterns and dynamics of V2's connections with other cortical areas, particularly to its major source of ascending input, area V1. As we have seen, the organization of information in area V1 and V2 is quite different. While in V1 color and orientation are largely segregated into the blob and interblob compartments, in V2 these properties are organized into the V2 stripes. The organization for properties such as ocular dominance, so prominent in V1, are completely absent in V2, wherein, instead, other properties such as disparity become well organized. These marked changes in organization lead to questions regarding how different types of information are redistributed and recombined as they pass from V1 to V2. One claim that has been made with respect to V1–V2 connections is that they maintain a segregation of color, form, and motion information. Another issue concerns the notion that the relationship between visual areas such as V1 and V2 is hierarchical and the flow of information is serial in nature. Below we review the evidence surrounding both of these questions and offer some further discussion on the issue of interareal processing.

5.1. Color, Form, and Motion: How Segregated Are They?

Anatomical studies have indicated a significant degree of segregation between the so-called color, form, motion, and depth pathways. As shown by sev-

eral studies, injections of anatomical tracers into the thin stripes in V2 preferentially label the blobs in V1, while injections into pale stripes in V2 preferentially label interblob regions in V1 (Livingstone and Hubel, 1984; Horton, 1984; DeYoe and Van Essen, 1985; Shipp and Zeki, 1985). Thick stripes in V2 receive inputs primarily from the magno-dominated layer 4B of V1 (Livingstone and Hubel, 1987a). Each of these stripes in turn has a different pattern of feedfoward connections with higher cortical areas. For example, the thin and pale stripes in V2 have interconnections with area V4 and thick stripes with area MT (Shipp and Zeki, 1985; DeYoe and Van Essen, 1985; Krubitzer and Kaas, 1990a,b; Nakamura *et al.,* 1993; DeYoe *et al.,* 1994). Within V4 there are segregated color and orientation patches (Ghose and Ts'o, 1997), consistent with the segregated connectivity of V4 with the V2 thin and pale stripes (DeYoe *et al.,* 1994).

Though the pattern of the V2–V1 feedback connections has not been well studied, the segregation between the blob–thin stripe connections and the interblob–pale stripe connections has been reported to be reciprocal in nature and patchy as well (Wong-Riley, 1979b; Livingstone and Hubel, 1984). Within the V1 intrinsic connections, the pattern of functional segregation is apparently maintained, since injections into blobs label neighboring blobs and avoid interblob regions, while those in interblobs label neighboring interblobs preferentially (Livingstone and Hubel, 1984). This anatomical pattern is also mirrored in the pattern of functional interactions as measured by single-unit physiology coupled with cross-correlation analysis (Ts'o and Gilbert, 1988). These findings as well as a number of psychophysical (e.g., Cavanagh, 1989; Livingstone and Hubel, 1987b) and clinical and human (Vaina *et al.,* 1990; Baker *et al.,* 1991; Haxby *et al.,* 1991; Zeki *et al.,* 1991; Tootell *et al.,* 1995) studies served as a basis for the idea that color, form, and disparity/motion information are processed in separate parallel visual pathways (Livingstone and Hubel, 1987b; DeYoe and Van Essen, 1988; cf. Merigan and Maunsell, 1993; Cavanagh, 1989):

	V1	V2	
Color	Blob	Thin stripe	V4 color patch
Orientation	Interblob	Pale stripe	V4 orientation patch
Motion/disparity	layer 4B	Thick stripe	MT

5.1.1. Segregation of M and P Inputs

The question of color, form, and motion segregation has been related to the functional and anatomical segregation of the magnocellular (M) and parvocellular (P) "pathways," so named for their laminar localization in the lateral geniculate nucleus (LGN). The P system has been proposed as the primary contributor of visual input to the ventral ("what") pathway, and is though to be responsible or form and color perception. The M system has been suggested to be the primary source to the dorsal pathway, which handles primarily motion and disparity information (for reviews see Livingstone and Hubel, 1988; Merigan and Maunsell, 1993). There are certain anatomical and functional grounds for these

claims. Anatomical studies suggest parallel and largely separate retinocortical pathways: the P pathway arises in the midget retinal ganglion cell and ascends through the parvocellular LGN to layer 4cβ in V1, both blobs and interblobs in V1, thin stripes and pale stripes of V2, V4, and the temporal lobe; the M pathway beings with the parasol retinal ganglion cell and continues to magnocellular LGN, layer 4Cα in V1, layer 4B in V1 and blobs in V1, thick stripes in V2, V3d, V5 (MT), and beyond, into parietal cortex. Further circumstantial evidence has been provided by the staining pattern for the antibody CAT 301 (Hockfield and McKay, 1983), which seems to selectively stain components of the M pathway, from the retina, through the magnocellular layers of the LGN, to the thick stripes of V2 and onward to V5 (MT) (DeYoe *et al.,* 1990; Krubitzer and Kaas, 1990a, b). From a functional standpoint, the most distinctive properties of the cells of the early P system, that of color opponency (Wiesel and Hubel, 1966), are indeed likely to be the source of the color input into the ventral stream (Merigan, 1989). Similarly, the specialization of the M system for the highest temporal properties (for review, see Shapley, 1990) are likely to be responsible for at least the fastest motion processing abilities of the dorsal pathway.

However, a number of studies now suggest that there is considerable mixing of M and P inputs in both the dorsal and ventral streams. In V1 it appears that blobs receive both M and P inputs (Lachica *et al.,* 1992; Edwards *et al.,* 1995) and, contrary to the initial anatomically based notions, M inputs contribute to both blobs and interblobs (Nealey *et al.,* 1991). In V2, evidence for further mixing occurs at places where thin and thick stripes merge, where patches of color disparity cells are found (Ts'o *et al.,* 1991). In V4, the inactivation of either M or P layer of the LGN significantly reduces responses of V4 cells (Ferrera *et al.,* 1992), thus indicating that this component of the ventral stream receives significant input from both M and P sources. However, responses of cells in V5 (MT) are strongly affected by M, but not P, inactivation (Maunsell *et al.,* 1991), suggesting that at least this component of the dorsal stream is M dominated. It has been shown that responses of single cells in the M pathway fall to a minimum with isoluminant chromatic stimuli, though residual frequency doubled responses may remain (Lee *et al.,* 1988; Gegenfurtner *et al.,* 1994; Dobkins and Albright, 1993). These observations along with psychophysical demonstrations of a reduction in motion perception near isoluminance suggest an absence of strong P input to MT. However, lesions to the P layers of the primate LGN are reported to severely affect high-spatial-frequency stereopsis (Schiller *et al.,* 1990), suggesting that for stereopsis, a property often associated with the dorsal pathway, there may be significant P input. Thus, the weight of evidence suggests that for most aspects of normal vision, both the P and M systems are likely to contribute in both the dorsal and ventral streams.

Similarly, several lines of evidence suggest that the notion of a strict segregation of form, color, motion, and depth processing is too simplistic a view. While it is clear that in V1 and V2 color, form, and motion are segregated, there is also clearly some degree of interaction between these pathways. Anatomically, within V2, for example, stripes are highly interconnected by horizontal connections (Ts'o *et al.,* 1991; Levitt *et al.,* 1994b; Malach *et al.,* 1994). Injections of tracer into any stripe result in patches of label in each of the other stripe types. Furthermore, both in V1 and V2, cells of mixed functional properties are often found. For example, color oriented cells are prominently found at the borders between thin and pale stripes in V2 (Ts'o *et al.,* 1991; Roe and Ts'o, 1995) and also in

periblob regions in V1 (Ts'o and Gilbert, 1988); color disparity cells have also been described at regions of merging between thin and thick stripes (Ts'o *et al.*, 1997). Other investigators have also emphasized that the spatial and temporal tuning properties of the cells found in each type of V2 stripe are quite similar (Levitt *et al.*, 1994a). Thus, although at the level of V2 the extent of functional and anatomical segregation is quite striking, there is also ample evidence that this segregation is not strict and the pathways for form, color, motion, and depth processing have substantial opportunities for interaction.

5.1.2. Specificity of Functional Interactions

Recent cross-correlation studies between V1 and V2 have added further insights into the interactions between V1 and V2 and the issue of segregation versus interaction. The strategy of Roe and Ts'o (1992, 1997) involved the use of multiple microelectrodes to target specific structures (such as blobs or interblobs in V1 or specific stripe compartments in V2) localized by optical imaging, followed by the functional characterization of single cells in each electrode and collection of spike trains in response to particular visual stimuli. Cross-correlation analysis was then applied to these spike trains to characterize the functional interactions between these pairs of identified cells. By inference, these interactions are also indicative of the connectivity between specific structures in V1 and V2, thus providing a functional correlate to known anatomical connections between V1 and V2.

By studying hundreds of cell pairs using this approach, certain patterns or rules of V1–V2 interactions have emerged (Fig. 14). Similar to the pattern of interactions found between V1–V1 cell pairs (Ts'o *et al.*, 1986; Ts'o and Gilbert, 1988), among oriented cells, peak correlograms were found primarily among V1–V2 cell pairs with matching orientation preference (Fig. 14A). However,

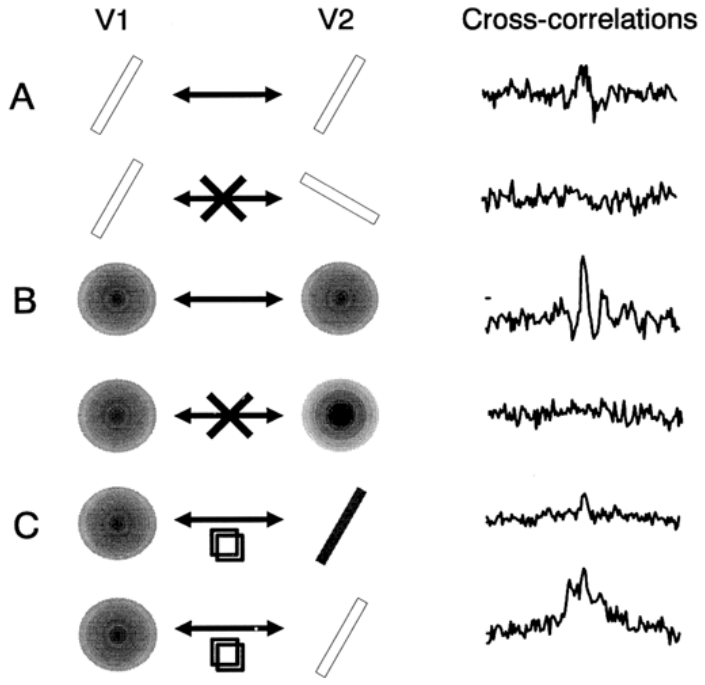

Figure 14. Summary of functionally specific V1–V2 interactions. Cell pairs are schematized in the left column and representative correlograms are shown in the right column. "Like to like" interactions are commonly seen: (A) Orientation-selective broadband cell pairs in V1 and V2 show peaked correlograms when orientation selectivities match, but flat correlograms otherwise. (B) Color-selective cell pairs interact only when color selectivities match. (C) While interactions in A and B do not require receptive field overlap, those between nonoriented color cells in V1 and oriented cells in V2 have a strong dependence on receptive field overlap.

such interactions were not restricted to those between interblobs and pale stripes. Interactions between broadband oriented cells in V1 interblobs and color oriented cells at thin/pale borders as well as disparity cells in thick stripes were also observed. In the color domain, peaked correlations occur most often between nonoriented color cells located in V1 blobs and cells in V2 thin stripes with similar color specificities (Fig. 14B). Interactions between nonoriented color cells in V1 blobs and oriented broadband cells in V2 pale stripes were also found (Fig. 14C). Cell pairs with dissimilar properties most often exhibited flat correlograms.

The presence of interaction apparently depended on receptive field overlap for certain functional pairings (Fig. 14C) but not for others. In some examples (such as color nonoriented V1–V2 cell pairs), interactions were found between V1–V1 pairs and V1–V2 pairs which had nonoverlapping receptive fields separated by several receptive field diameters. For other functional cell pairings, such as nonoriented V1 color cell paired with an oriented V2 color cell, interactions were only observed when there was significant receptive field overlap. This differing dependence on receptive field overlap suggests that different functional compartments within the stripes may have differing degrees of spatial divergence and convergence.

While these results may be viewed as supportive of the general notion of functional segregation, a more comprehensive examination of the data reveals that different receptive field types within a single stripe type may exhibit different patterns of connectivity, some of which may conform to the notion of segregation and others which may not. The possibility that there are more than three pathways (e.g., a color oriented pathway?) should also be considered. And finally, even cells which appear functionally similar may in fact be part of different pathways. For example, it is possible that one class of broadband oriented cell in V2 may simply have its properties conferred on it by other broadband oriented cells in V1, and another broadband oriented cell class be constructed from converging nonoriented broadband (or color) inputs. Thus there is a great deal of complexity in the details of functional connectivity that make "segregated or not segregated" an overly simplistic question.

5.1.3. Dynamics

Yet another aspect of cortical connectivity that greatly increases the complexity of the issue is the dynamic nature of these connections. For example, cross-correlation studies have reported dramatic changes in V1–V2 effective connectivity, including strengthening, weakening, as well changes in the signature and oscillatory characteristics of V1–V2 correlograms (Nelson *et al.,* 1992; Frien *et al.,* 1994; Ts'o *et al.,* 1993; Roe and Ts'o, 1997). These changes are thought to reflect a modulation or shift in synaptic efficacy or coupling. The changes may be context or stimulus dependent, or may relate to attentional or behavioral state (cf. Gilbert and Wiesel, 1990; Knierem and Van Essen, 1992; Lamme, 1995). For example, among color cells, the type of color stimuli influenced the shape and strength of the correlogram (Roe and Ts'o, 1997; Fig. 15). Continuity of contour may be another example of context dependence, and has been linked to perceptual binding (Gray and Singer, 1989; Nowak *et al.,* 1995b;

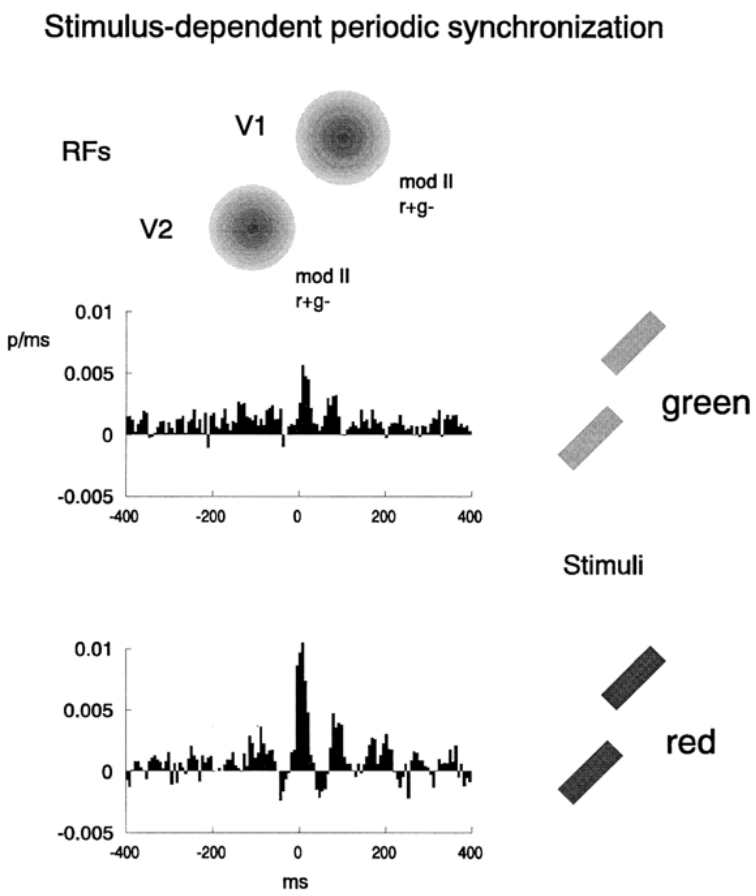

Figure 15. Stimulus dependence in the color domain. Two nonoverlapping red on-center/green off-center color-opponent cells, one in V1 and one in V2. The correlograms were significantly stronger and exhibited more periodicity when stimulated with red moving bars (below) than with green (above), even though both stimuli drove the cell pair nearly equally well, with similar resulting firing rates.

Ts'o *et al.*, 1993; Roe and Ts'o, 1997). Importantly, it appears that the dynamics may be functionally specific, being more prevalent for some cell types than others. Interactions between orientation-selective cells can be influenced by the orientation of presented stimulus. Interactions between color-selective cells are changed by stimulus color. It is also conceivable that, for example, an oriented V2 cell is signalled by orientation information in V1 under one stimulus condition and convergent color cells under another. Thus the finding that these large V1–V2 networks might change or reconfigure themselves in very specific ways depending on state or context suggests ongoing and frequent shifts in the degree of functional segregation of the form, color, motion, and depth pathways during normal vision and visually guided behavior.

In considering the overall task of visual perception, the question of whether the color, form, and motion/disparity pathways are segregated must be considered too simplistic. For example, there is physiological and anatomical evidence that columns of cells tuned for a particular orientation are interconnected not only within a single area (e.g., V1), but across corticocortical boundaries (e.g.,

V1–V2). In one sense then, the degree of functional segregation, in view of this general rule of like-to-like connectivity, is even higher than that suggested by the generally more macroscopic anatomical studies. On the other hand, when one considers, for example, that a color border might appear as part of the foreground in one context and part of the background in another, it becomes clear that dynamic interactions between color and form are necessary to define and interpret that border, and that strict functional segregation is not workable. Thus, while at early stages there may be a significant extent of segregation between color, form, and motion/disparity, interactions between these pathways must become an increasingly crucial aspect of higher order visual processing.

5.2. Serial or Parallel?

5.2.1. Traditional Hierarchical View

The hierarchical view of the architecture of visual cortical processing is in part based on the observation that outputs from upper cortical layers of "lower" cortical areas terminate in layer 4 of "higher" cortical areas, and feedback from "higher" areas originate and project to layers other than layer 4 (Rockland and Pandya, 1979; Maunsell and Van Essen, 1983; Felleman and Van Essen, 1991). In considering the interconnectivity of V1 and V2, projections from V1, arising primarily from layers 2, 3, 4A, and 4B in V1, terminate primarily in layers 3B and 4 in V2 both in the macaque (Lund *et al.,* 1981; Livingstone and Hubel, 1984, 1987a; Kennedy and Bullier, 1985; Van Essen, *et al.,* 1986; Rockland, 1992) and in the squirrel monkey (Spatz *et al.,* 1970; Wong-Riley, 1979b; Tigges *et al.,* 1981; Fitzpatrick *et al.,* 1983; Rockland, 1992). Feedback projections from V2 arise primarily in layer 6, though also in layer 3A in V2, and terminate in layers 1, 5, and 6 in V1 (Rockland and Virga, 1989; Weller and Kaas, 1983).

The hierarchical view of the visual cortical pathways leads to the expectation that V2 is higher in the cortical hierarchy than V1 and that it receives its primary driving input from V1. This is consistent with the fact that virtually all ascending input, with the exception of some relatively sparse input from the pulvinar (Curcio and Harting, 1978; Horton, 1984), to V2 is provided by V1. Inactivation of V1 clearly silences cells in V2, including those in all three compartments (Schiller and Malpeli, 1977; Girard and Bullier, 1989), thus demonstrating that V1 input to V2 is necessary for the activation of V2 neurons. It is likely that other inputs to V2, such as those from the pulvinar, V4, or MT, may provide only a modulatory role which alone are not sufficient to drive V2 cells.

5.2.2. Parallel Processing in V1 and V2

5.2.2a. Inactivation Studies. Further physiological examination of this issue, however, has put this strict hierarchical scheme into question. While inactivation of V1 silences V2, the effect of V2 inactivation on V1 can also be profound. Both supragranular and infragranular layer responses in V1 are also vastly reduced by V2 inactivation with either cooling or cobalt chloride lesion methods (Sandell and Schiller, 1982; Mignard and Malpeli, 1991). In addition, Mignard and Malpeli (1991) report that following inactivation of LGN with ibotenic acid lesions, receptive field properties, such as orientation selectivity, of

V1 cells outside of layer 4 remain intact; additional cobalt chloride lesions of V2 lead to profound shutdown of V1 responsiveness, suggesting that V2 can be a major driving source for V1 cells.

5.2.2b. Latency Studies. Studies of visual latencies of cells in V1 and V2 suggest that much neuronal activation occurs simultaneously in V1 and V2 (Raiguel *et al.,* 1989; Nowak *et al.,* 1995a). Neuronal activation latencies (as measured by onset of response to flashing spots or bars) of V1 cells are shortest in layer 4Cα and layer 4B (Maunsell and Gibson, 1992) and precede the shortest latencies in V2 (which surprisingly occur in the infragranular layers) by up to 10 msec. While it is true that as a population, V2 cells lag those of V1 cells, neuronal latency distributions in V1 and V2 overlap greatly such that by the time half of the sampled V2 population has responded, roughly half the cells in V1 have yet to respond (Nowak *et al.,* 1995a). This is true even within each of the color and motion channels. Layer 4B latencies in V1 have great overlap with those of thick stripes in V2, as do supragranular layer cells in V1 (which would include those of both blob and interblob cells) and those in thin and pale stripes in V2 (compare Nowak *et al.,* 1995a, Fig. 5 to Munk *et al.,* 1995, Fig. 3A). Cross-correlation studies of V1–V2 cell pairs also indicate that the predominant contributor to V1–V2 interaction is common input (Roe and Ts'o, 1992, 1997; see also Nelson *et al.,* 1992).

5.2.2c. Sources of Common Input. Possible sources of common input to V1 and V2 are numerous, both cortically and subcortically. The most prevalent source of common input to V1 and V2 may well be other projection neurons within V1 and V2. These are typically pyramidal cells in the supra- or infragranular layers, which are known to have dense local axonal plexuses (e.g., Valverde, 1985). Other possible sources are much less prominent and unlikely to form major sources of the common input observed. In double-labeling studies with fluorescent tracer injections into V1 and V2, Kennedy and Bullier (1985) report that on the order of 10% of all labeled neurons in the lateral and inferior pulvinar and the claustrum were double-labeled. Inputs from the LGN, however, are segregated with inputs to V1 arising primarily from the magno and parvo layers and those to V2 from the interlaminar S layers (Bullier and Kennedy, 1983). In other cortical areas, neurons which bifurcate to both V1 and V2 reside primarily in the infragranular layers of the anterior lunate, the prelunate gyrus, and the superior temporal sulcus. These include areas V3, V4, MT, TEO, as well as others (Van Essen, 1985; Rockland *et al.,* 1994).

5.2.2d. Network Size. Another striking observation is that correlograms between V1–V2 cell pairs are often quite broad in comparison to the V1–V1 cell pairs (cf. Ts'o *et al.,* 1986), indicating a greater temporal dispersion in V1–V2 interactions. Figure 16 shows a comparison of typical correlogram peak widths between V1–V1, V1–V2, and V2–V2 cell pairs. The V1–V1 correlogram peak widths typically fall in the range of 2–10 msec (Ts'o *et al.,* 1986; Ts'o and Gilbert, 1988). The V1–V2 correlogram peak widths, in contrast, are typically 30–50 msec and range quite broadly up to 100 msec or more. The V2–V2 correlogram peaks as a whole also tend to be sharper than V1–V2 interactions, and range

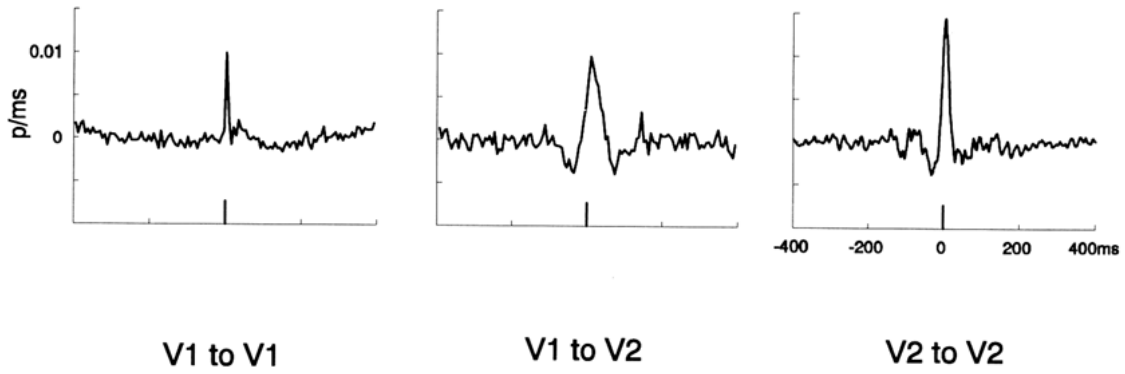

Figure 16. Comparison of V1–V1, V1–V2, and V2–V2 correlogram peak widths. V1–V2 correlogram peaks are much broader than those of either V1–V1 or V2–V2 peaks, indicating a greater temporal dispersion in corticocortical connections. Peak widths of V1–V1 (left), V1–V2 (middle), and V2–V2 correlograms shown are 10, 50, and 20 msec, respectively.

from 5 to 20 msec. These results indicate that V1–V2 interactions are much more temporally dispersed than either V1–V1 or V2–V2 interactions. This greater temporal dispersion suggests that V1–V2 interactions, and perhaps corticocortical interactions in general, are part of larger, more complex cortical networks than the cortical circuitry intrinsic to a single area.

5.2.3. Revised View of Interareal Interaction

The overwhelming prevalence of common input interactions (Nelson *et al.*, 1992; Roe and Ts'o, 1992, 1997) raises questions concerning the relative roles of V1 and V2 in the transfer and transformation of incoming visual inputs. One traditional view of cortical processing has held that, since visual information to higher cortical areas passes through V1, information passes more or less serially from V1 to V2. This view has been strengthened as well by anatomical studies suggesting segregated channeling of visual information from V1 to V2. However, findings that V1 and V2 cells are often simultaneously activated lead to a slightly different view of corticocortical connectivity. Perhaps cortical areas should not be considered separate entities linked by a few functional streams, but rather they should be regarded as highly coupled and interdependent coprocessors. Instead of passively transmitting or replicating the outputs of V1 in the input layer of V2, the interareal connections themselves could participate significantly in computational transformations, bringing about the generation of new receptive field properties. These observations suggest that cortical areas process at least a portion of visual information concurrently, in parallel, and serve to deemphasize a serial or hierarchical view.

6. Relationship of Structure and Circuitry to Perception

6.1. The Role of V2 in Perceptual Binding across Modalities

In the past several sections, we have noted that while the extent of segregation of the form, color, motion, and depth pathways is remarkable, there is also

substantial evidence for interaction and cooperativity between these pathways. These themes continue in higher areas such as V4 and MT. Consistent with physiological characteristics of cells in V4 and MT, V4 receives anatomical inputs preferentially from the thin and pale stripes of V2, while MT receives projections from thick stripes in V2 (DeYoe and Van Essen, 1985; Shipp and Zeki, 1985, 1989; DeYoe *et al.,* 1994). The functional segregation that occurs in V2 allows the distribution of visual information to either the ventral ("what") or dorsal ("where") pathways. Thus, V2 sits at an important juncture in the information flow to other cortical areas. Its position in the cortical hierarchy would be well suited to the context-dependent gating of ascending information. Given its position, V2 conceivably could play a crucial role, via feedback connections, in the binding of what and where percepts.

The multiple, interleaved mapping architecture of V2 may be ideally suited for stripe–stripe interactions that may contribute to perceptual binding. Several lines of evidence suggest that such functional binding could take place via horizontal connections within V2. Injections of anatomical tracers into V2 stripes revealed patches of label contained primarily within the injected stripe cycle (i.e., within 4 mm of the injection site; Amir *et al.,* 1993; Levitt *et al.,* 1994b). Furthermore, these patches occurred both within the stripe injected and within each of the other two stripe types (Ts'o *et al.,* 1991; Levitt *et al.,* 1994b; Malach *et al.,* 1994). Supplementing these anatomical findings are functional studies using cross-correlation analysis that also demonstrate interactions between different stripe compartments in V2 up to a distance of several stripes (Roe and Ts'o, 1992, 1997). Therefore V2 seems to possess the functional and topographic architecture to contribute to the perceptual binding of the submodalities of visual information.

6.2. Role of V2 in Contour Perception: An Implementation

In this section, as a way of summarizing, we give an example of how the organization and circuitry discussed in this chapter might be used to help construct a coherent view of object contours. These suggestions are not meant to be a comprehensive summary of all that V2 does. That is, contour identification is by no means the only or even the primary role of V2, as V2 is also likely to be involved in other aspects of visual processing.

One of the primary functions of the visual system is the identification of objects. Inherent in object identification is the delineation of object contour for the purposes of figure–ground segregation. It has been proposed (Cavanagh, 1989) from psychophysical studies that the visual system initially encodes two-dimensional shape in several different domains (including those of luminance, color, texture, motion, and binocular disparity) which are subsequently abstracted to generate a generalized shape representation. Such a "segregate and generalize" strategy has also been proposed for the representation of three-dimensional surfaces (Carman and Welch, 1992). However, the cortical locus of these events is unknown. We propose that area V2 may play a key role in the extraction of generalized shape information from the visual scene. Specifically, the evidence reviewed in this chapter suggests that V2 is involved in the extraction of higher order contour information using inputs from several different

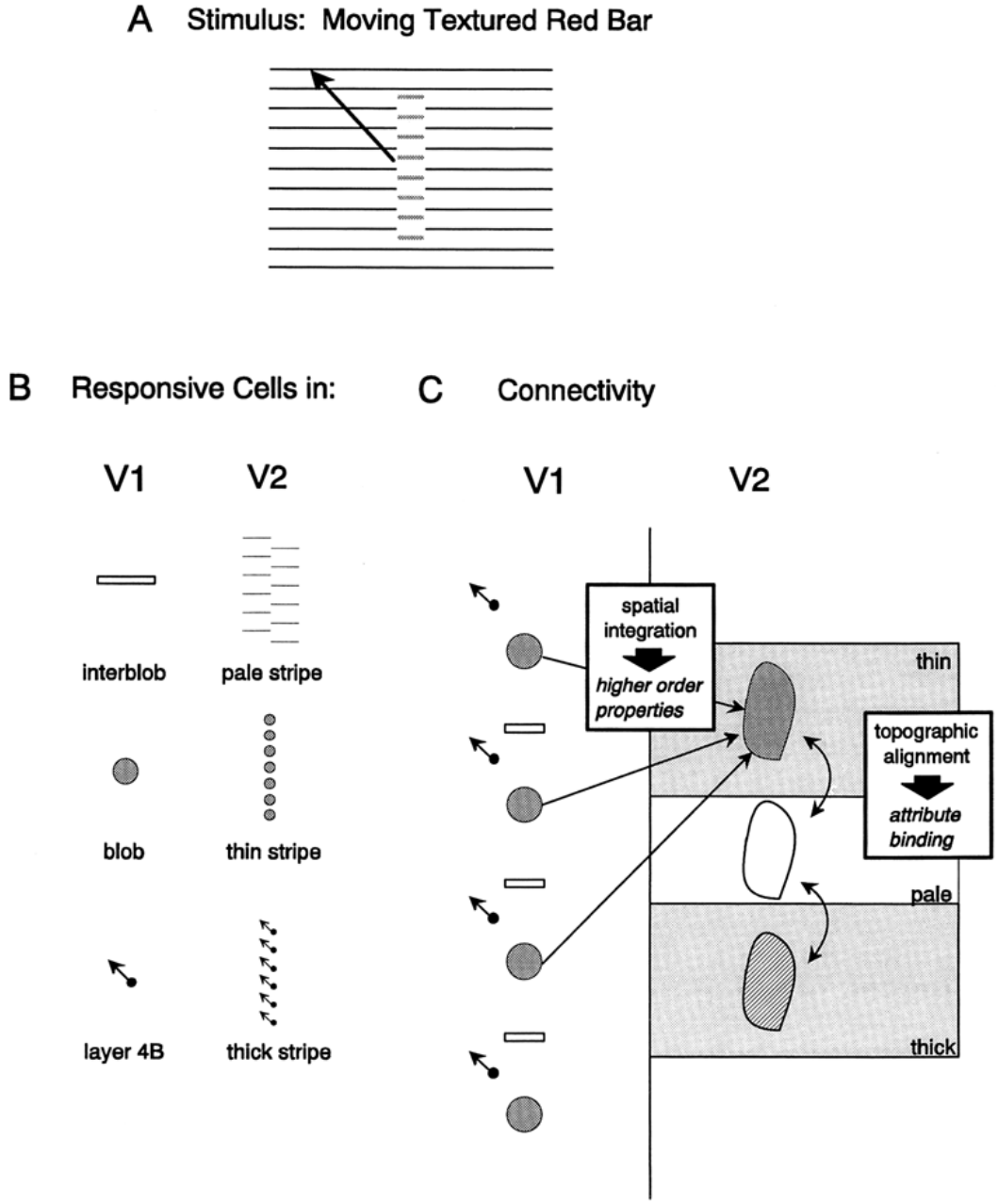

Figure 17. Building of object contour representation by V2 organization and circuitry. How V2 sees a red bar moving in space. (A) The stimulus is a red bar moving in space whose borders are defined by color, by illusory contours, and by motion and depth cues. (B) V1 cells and V2 cells see different aspects of this stimulus. In V1, the following cells are responsive to this stimulus: interblob cells with horizontal orientation selectivity, blob cells with red selectivity, motion cells with upward and leftward direction, and perhaps disparity cells of the appropriate disparity selectivity (not shown). In V2, there are more-specialized cells which see higher order features of this stimulus: illusory contour cells in pale (and perhaps thick) stripes with vertical orientation selectivity, color oriented cells (at pale/thin stripe border zones) with vertical orientation selectivity, disparity cells in thick stripes with appropriate disparity selectivity (not shown). Response to the vertical motion contrast border may be encoded by either motion coherence cells in V2 (Peterhans and von der Heydt, 1993) or by MT cells. (C) Possible circuitries between V1 and V2 cell populations. Convergent connections (large arrows) from functionally specific V1 sites serve, either directly or indirectly, to generate higher order receptive field properties in V2 which require spatial integration. Interstripe connections in V2 serve to ensure close visuotopic alignment of multiple views and contribute to perceptual unity.

submodalities, the segregation of the visual scene into multiple views, and the alignment of these multiple views. This example is illustrated in Fig. 17.

6.2.1. Feature (Contour) Extraction within Separate Functional Domains

In Fig. 17A we depict a red bar moving in space whose borders are defined by color, by illusory contours, and by motion and depth cues. In V1, several different cell types (Fig. 17B) are responsive to this stimulus: interblob cells with horizontal orientation selectivity (possibly end-stopped), nonoriented blob cells with red selectivity, motion cells selective for upward and leftward direction, and disparity cells of the appropriate disparity selectivity. In V2, there are more specialized cells which see higher order features of this stimulus: illusory contour cells in pale (and perhaps thick) stripes with vertical orientation selectivity, color oriented cells (at pale/thin stripe border zones) with vertical orientation selectivity, and disparity and motion contrast cells which also signal vertical orientation. The presence of this contour is thus signalled in several different ways within V2.

Connections between these several cell populations are illustrated in Fig. 17C (arrows indicate either direct or indirect connections). Red-selective blob cells in V1 may converge, either directly or indirectly, onto a single red orientation-selective cell either in a V2 thin stripe or at a color orientation-selective cluster at a thin/pale border. End-stopped V1 cells located in interblobs which are broadband and selective for horizontal orientations may converge to generate vertically oriented illusory contour cells in V2 pale stripes (cf. Peterhans and von der Heydt, 1989). Motion-selective cells in layer 4B of V1 which prefer motion in the upward and leftward directions may converge onto cells in V2 thick stripes or in MT which signal the presence of a vertical motion border. Similarly, perhaps via additional circuitry within V2, the convergence of disparity information from the two eyes may signal the presence of a disparity contour (not shown). As we have seen from both anatomical and functional connectivity studies, each of the three stripe systems in V2 serves to collect, in a convergent fashion, functionally specific information from V1. The purpose of collecting this information across an expanse of V1 into a single large stripe may be to construct higher order receptive fields that integrate across spatially distributed local detectors, such as the elements forming an illusory contour percept.

6.2.2. Topographic Alignment of Multiple Views

Given this decomposition into multiple views, by what mechanism does the visual system know that these three representations refer to the same contour in space? A likely candidate for bringing these three representations together is the extensive network of clustered interconnections between the three functional stripe types. These horizontal connections, which extend primarily to within a single stripe cycle, could serve to bind the several attributes together within a stripe cycle and thereby provide close visuotopic alignment of the different visual maps (Fig. 17C). The thin/pale/thick/pale stripe set is thus a functional unit which shares and processes contour information in concert. The output of

such processing in V2 may then serve to produce an abstracted contour representation of a vertical bar at a higher cortical level.

7. Why Another Stage of Cortical Processing Apart from V1?

Thus far, we have skirted around the question as to the raison d'être for V2, and more generally, the principles for the existence of multiple visual areas. This question is perhaps particularly pertinent in the case of V2, given that the types of visual inputs and outputs for V1 and V2 are quite similar and both subserve both the dorsal and ventral visual pathways. Several notions of the functional role of V2 and the necessity for multiple visual areas in general revolve around the idea that a single cortical area is limited in the amount and extent of processing and transformations it can perform, either spatially or computationally or both. A complex computational task such as those required for vision may be too difficult or impossible for one area to handle, or may be biologically/developmentally "easier" to distribute among several cortical areas. A few lines of circumstantial evidence can be offered:

1. The continued elaboration from area to area of higher order receptive field properties, particularly those that integrate information across an increasing extent of visual space. This trend may be viewed as multiple representations in scale. This observation might suggest that the computational demands of the task require more machinery than a single cortical area possesses or can easily mobilize.

2. The establishment of distinctive cortical organizations for a different mix of functional properties from area to area. Functional properties that are organized in one area may not be organized in a "higher" area even though that functional property may be present. New types of functional organization often emerge, instead, in the higher area.

3. The apparent conservation from area to area in the extent and character of the intrinsic anatomical connections, and similarly the stereotyped nature of cortical circuitry. These presumably biological/developmental limitations must set an upper bound as to how much a single cortical area can accomplish.

4. Despite the hierarchical evidence that implies a serial flow of information from V1 to V2, other physiological results suggests that visual input arrives in V2 at nearly the same time as in V1 and therefore should permit processing in V2 to occur largely in parallel to that in V1.

5. The anatomical and physiological nature of corticocortical connections is quite different from that of connections and intrinsic circuitry within a cortical area. Therefore the computational capabilities and the nature of the interactions between different functional units within a single cortical area versus units distributed in separate cortical areas are likely to be quite different.

Given these observations, we further suggest that:

1. There are limits for a single cortical area in the number of different representations of visual information possible in the cortical architecture.

2. There is a computational payoff in using multiple intermediate representations for the ease of computing different transformations on the visual information.

3. There are biophysical/energetic/developmental pressures that favor cortical representations that are implemented as columns or clusters of neighboring neurons rather than as spatially dispersed or disorganized ensembles.

4. The nature of corticocortical connections may be more suited to a restricted or different class of computations or information transfer, perhaps including those employed by computational units that are loosely coupled and operate in parallel.

5. Certain aspects of the whole computational task are more easily separable and parallelized, and together with the considerations of differences between corticocortical and intrinsic circuitry, may dictate which aspects or submodalities are explicitly represented, parallelized, and delegated to different cortical areas. In other words, some computations are so inherently interactive that the implementing circuits must reside within the same cortical area, while others may be more easily broken down into intermediate computations that are more easily distributed across separate cortical areas.

These ideas and observations prompt us to suggest that the biological pressure to create a V2 stems from the computational limitations of a single cortical area and the need for a number of different intermediate representations. The advantages of using well-chosen intermediates toward tackling a complex problem can be found in many disciplines, such as engineering, chemistry, and of course mathematics. Such intermediate forms often transform a difficult task into a much easier procedure. Similarly, cortical areas such as V1 and V2 may be viewed as platforms for staging the computational problem in terms of useful intermediates so as to facilitate parallel processing and ultimately the completion of vision further down the visual pathways. For example, the extraction of perceptual contours in a visual scene might be staged by computing the distribution of the orientation of edges (defined by luminance, color, etc.), one useful intermediate, and then from orientation proceeding with endstopping and curvature, perhaps another useful intermediate, and then onto the incorporation of illusory contours and the binding of local features to extract a more global contour. Several of these stages of the overall computation and their intermediate results are sufficiently independent so as to facilitate their implementation in separate cortical areas, and separate functional modules within these cortical areas.

The available visual information to V1 and V2 is similar if not essentially identical, yet the mix of functional properties that are organized in each area are different. Both V1 and V2 have disparity cells and end-stopped cells, but only in V2 does a clear organization for these properties emerge. Both V1 and V2 contain directionally selective cells, yet only in V5 (MT) does a clear columnar organization for directionality emerge. On the other hand, V1 contains the most precise retinotopy, as well as the only organization for ocular dominance. These observations suggest not only that no single area can provide all the explicit representations necessary to facilitate visual processing, but that there is a natural sequence or succession of computations and their resultant intermediate forms in visual processing. If some of these intermediates can be built and used concurrently (in parallel), so much the better.

In this context, we restate some observations from a previous section by noting that nowhere beyond V2 in the visual hierarchy does the early and separate computations on form, color, disparity, and motion ever again benefit from

the possibilities for close interaction as in the neighboring stripes of V2. Thus an attractive view as to the special role of V2 is as an area for the staging of the intermediates of visual computation, promoting the parallelization of the processing of certain visual submodalities, and facilitating interactions and perhaps binding among these segregated submodalities, in preparation for their distribution to the even more separate dorsal and ventral pathways.

8. References

Allman, J. M., and Kaas, J. H., 1971, Representation of the visual field in striate and adjoining cortex of the owl monkey (*Aotus trivirgatus*), *Brain Res.* **35:**89–106.

Allman, J. M., and Kaas, J. H., 1974, The organization of the second visual area (V-II) in the owl monkey: A second order transformation of the visual hemifield, *Brain Res.* **76:**247–265.

Amir, Y., Harel, M., and Malach, R., 1993, Cortical hierarchy reflected in the organization of intrinsic connections in macaque monkey visual cortex, *J. Comp. Neurol.* **334:**19–46.

Baizer, J. S., Robinson, D. L., and Dow, B. M., 1977, Visual responses of area 18 neurons in awake, behaving monkey, *J. Neurophysiol.* **40:**1024–1037.

Baker, C. L., Hess, R. F., and Zihl, J., 1991, Residual motion perception in a "motion-blind" patient, assessed with limited-lifetime random dot stimuli, *J. Neurosci.* **11:**454–461.

Blasdel, G. G., and Fitzpatrick, D., 1984, Physiological organization of layer 4 in macaque striate cortex, *J. Neurosci.* **4:**880–895.

Brodmann, K., 1909, *Vergleichende Lokalisationslehr der Grosshirnrinde,* Barth, Leipzig.

Bullier, J., and Kennedy, H., 1983, Projection of the lateral geniculate nucleus onto cortical area V2 in the macaque monkey, *Exp. Brain Res.* **53:**168–172.

Carman, G. J., and Welch, L., 1992, Three-dimensional illusory contours and surfaces, *Nature* **360:**585–587.

Cavanagh, P., 1989, Multiple analyses of orientation in the visual system, in: *Neural Mechanisms of Visual Perception* (D. M. Lam and C. D. Gilbert, eds.), Portfolio, Woodlands, TX, pp. 261–279.

Cowey, A., 1964, Projection of the retina on to striate and prestriate cortex in the squirrel monkey, *Saimiri sciureus, J. Neurophysiol.* **27:**366–393.

Curcio, C. A., and Hartin, J. K., 1978, Organization of pulvinar afferents to area 18 in the squirrel monkey: Evidence for stripes, *Brain Res.* **143:**155–161.

Daniel, P. M., and Whitteridge, D., 1961, The representation of the visual field in the cerebral cortex in monkeys, *J. Physiol.* (Lond.) **159:**302–321.

DeYoe, E. A., and Van Essen, D. C., 1985, Segregation of efferent connections and receptive field properties in visual area V2 of the macaque, *Nature* **317:**58–61.

DeYoe, E. A., and Van Essen, D. C., 1988, Concurrent processing streams in monkey visual cortex, *Trends Neurosci.* **11:**219–226.

DeYoe, E. A., Hockfield, S., Garren, H., and Van Essen, D. C., 1990, Antibody labeling of functional subdivisions in visual cortex: Cat-301 immunoreactivity in striate and extrastriate cortex of the macaque monkey, *Visual Neurosci.* **5:**67–81.

DeYoe, E. A., Felleman, D. J., Van Essen, D. C., and McClendon, E., 1994, Multiple processing streams in occipitotemporal visual cortex, *Nature* **371:**151–154.

Dobkins, K. R., and Albright, T. D., 1993, What happens if it changes color when it moves? The nature of chromatic input to macaque visual area MT, *J. Neurosci.* **14:**4854–4870.

Dow, B. M., Snyder, A. Z., Vautin, R. G., and Bauer, R., 1981, Magnification factor and receptive field size in foveal striate cortex of the monkey, *Exp. Brain Res.* **44:**213–228.

Edwards, D. P., Purpura, K. P., and Kaplan, E., (1995), Contrast sensitivity an spatial frequency response of primate cortical neurons in and around the cytochrome blobs, *Vision Res.* **35:**1501–1523.

Felleman, D. J., and Van Essen, D. C., 1991, Distributed hierarchical processing in the primate cerebral cortex, *Cerebral Cortex* **1:**1–47.

Ferrera, V. P., Nealey, T. A., and Maunsell, J. H. R., 1992, Mixed parvocellular and magnocellular geniculate signals in visual area V4, *Nature* **358:**756–758.

Fitzpatrick, D., Itoh, K., and Diamond, I. T., 1983, The laminar organization of the lateral geniculate body and the striate cortex in the squirrel monkey (Saimiri sciureus), *J. Neurosci.* **3:**673–702.

Frien, A., Eckhorn, R., Bauer, R., Woelber, T., and Kehr, H., 1994, Stimulus-specific fast oscillations at zero phase between visual areas V1 and V2 of awake monkey, *NeuroReport,* in press.

Frostig, R. D., Lieke, E. E., Ts'o, D. Y., and Grinvald, A. M., 1990, Cortical functional architecture and local coupling between neuronal activity and the microcirculation revealed by *in vivo* high-resolution optical imaging of intrinsic signals, *Proc. Natl. Acad. Sci. USA* **87:**6082–6086.

Gattass, R., Gross, C. G., and Sandell, J. H., 1981, Visual topography of V2 in the macaque, *J. Comp. Neurol.* **201:**519–539.

Gegenfurtner, K. R., Kiper, D. C., Beusmans, J. M. H., Caradini, M., Zaidi, Q., and Movshon, J. A., 1994, Chromatic properties of neurons in macaque MT, *Visual Neurosci.* **11:**455–466.

Ghose, G. M., and Ts'o, D. Y., 1997, Form processing modules in primate area V4, *J. Neurophysiol.* **77:**2191–2196.

Gilbert, C. D., and Wiesel, T. N., 1990, The influences of contextual stimuli on the orientation selectivity of cells in primary visual cortex of the cat, *Vision Res.* **11:**1689–1701.

Girard, P., and Bullier, J., 1989, Visual activity in area V2 during reversible inactivation of area 17 in the macaque monkey, *J. Neurophysiol.* **62:**1287–1302.

Gray, C. M., and Singer, W., 1989, Stimulus-specific neuronal oscillations in orientation columns of cat visual cortex, *Proc. Natl. Acad. Sci. USA* **86:**1698–1702.

Grinvald, A., Lieke, E., Frostig, R. D., Gilbert, C. D., and Wiesel, T. N., 1986, Functional architecture of cortex revealed by optical imaging of intrinsic signals, *Nature* **324:**361–364.

Grinvald, A., Frostig, R. D., Lieke, E., and Hildesheim, R., 1988, Optical imaging of neuronal activity, *Physiol. Rev.* **68:**1285–1365.

Grinvald, A., Lieke, E. E., Frostig, R. D., and Hildesheim, R., 1994, Cortical point-spread function and long-range lateral interactions revealed by real-time optical imaging of macaque monkey primary visual cortex, *J. Neurosci.* **14:**2545–2568.

Guld, C., and Bertulis, A., 1976, Representation of fovea in the striate cortex of vervet monkey, cercopithecus aethiops pygerythrus, *Vision Res.* **16:**629–631.

Haxby, J. V., Grady, C. L., Horwitz, B., Ungerleider, L. G., Mishkin, M., Carson, R. E., Herscovitch, P., Schapiro, M. B., and Rapoport, S. I., 1991, Dissociation of object and spatial visual processing pathways in human extrastriate cortex, *Proc. Natl. Acad. Sci. USA* **88:**1621–1625.

Hockfield, S., and McKay, R. D. G., 1983, A surface antigen expressed by a subset of neurons in the vertebrate central nervous system, *Proc. Natl. Acad. Sci. USA* **88:**1621–1625.

Horton, J., 1984, Cytochrome oxidase patches: A new cytoarchitectonic feature of monkey visual cortex, *Phil. Trans. R. Soc. Lond.* **304:**199–253.

Horton, J., and Hubel, D. H., 1981, A regular patchy distribution of cytochrome-oxidase staining in primary visual cortex of the macaque monkey, *Nature* **292:**762–764.

Hubel, D. H., and Livingstone, M. S., 1984, Complex-unoriented cells in a subregion of primate area 18, *Nature* **315:**325–327.

Hubel, D. H., and Livingstone, M. S., 1984, Segregation of form, color, and stereopsis in primate area 18, *J. Neurosci.* **7:**3378–3415.

Hubel, D. H., and Wiesel, T. N., 1970, Cells sensitive to binocular depth in area 18 of the macaque monkey cortex, *Nature* **225:**41–42.

Hubel, D. H., and Wiesel, T. N., 1974, Uniformity of monkey satiate cortex: A parallel relationship between field size, scatter, and magnification factor, *J. Comp. Neurol.* **158:**295–305.

Hubel, D. H., and Wiesel, T. N., 1977, Functional architecture of macaque monkey visual cortex, *Proc. R. Soc. Lond. B* **198:**1–59.

Hubel, D. H., Wiesel, T. N., and LeVay, S., 1974, Visual field representation in layer IVC of monkey striate cortex, in: *Society for Neuroscience, 4th Annual Meeting, St. Louis,* Abstract 264.

Humphrey, A. L., and Hendrickson, A. E., 1983, Background and stimulus-induced patterns of high metabolic activity in the visual cortex (area 17) of the squirrel and macaque monkey, *J. Neurosci.* **3:**345–358.

Kennedy, H., Bullier, J., 1985, A double-labeling investigation of the afferent connectivity to cortical areas V1 and V2 of the macaque monkey, *J. Neurosci.* **5:**2815–2830.

Knierem, J. J., and Van Essen, C. D., 1992, Neuronal responses to static texture patterns in area V1 of the alert macaque monkey, *J. Neurophysiol.* **67:**961–980.

Krubitzer, L. A., and Kaas, J. H., 1989, Cortical integration of parallel pathways in the visual system of primates, *Brain Res.* **478:**161–165.

Krubitzer, L. A., and Kaas, J. H., 1990a, Cortical connections of MT in four species of primates: Areal, modular, and retinotopic patterns, *Visual Neurosci.* **5:**165–204.

Krubitzer, L., and Kaas, J. H., 1990b, Convergence of processing channels in the extrastriate cortex of monkeys, *Visual Neurosci.* **5:**609–613.

Lachica, E. A., Beck, P. D., and Casagrande, V. A., 1992, Parallel pathways in macaque monkey striate cortex: Anatomically defined columns in layer III, *Proc. Natl. Acad. Sci. USA* **89:**3566–3570.

Lamme, V. A., 1995, The neurophysiology of figure–ground segregation in primary visual cortex, *J. Neurosci.* **15:**1605–1615.

Landisman, C. E., Roe, A. W., and Ts'o, D. Y., 1994, The relationship of receptive field coverage to functional modules in primate V1, *Soc. Neurosci. Abstr.* **20:**1477.

Lee, B. B., Martin, P. R., and Valberg, A., 1988, The physiological basis of heterochromatic flicker photometry demonstrated in the ganglion cells of the macaque retina, *J. Physiol.* **404:**323–347.

Lennie, P., Krauskopf, J., and Sclar, G., 1990, Chromatic mechanisms in striate cortex of macaque, *J. Neurosci.* **10:**649–669.

LeVay, S., and Voigt, T., 1988, Ocular dominance and disparity coding in cat visual cortex, *Visual Neurosci.* **1:**395–414.

Leventhal, A. G., Thompson, K. G., Liu, D., Zhou, Y., and Ault, S. J., 1995, Concomitant sensitivity to orientation, direction, and color of cells in layers 2, 3, and 4 of monkey striate cortex, *J. Neurosci.* **15:**1808–1818.

Levitt, J. B., Kiper, D. C., and Movshon, J. A., 1994a, Receptive fields and functional architecture of macaque V2, *J. Neurophysiol.* **71:**2517–2542.

Levitt, J. B., Yoshioka, T., and Lund, J. S., 1994b, Intrinsic cortical connections in macaque visual area V2: Evidence for interaction between different functional streams, *J. Comp. Neurol.* **342:**551–570.

Levitt, J. B., Yoshioka, T., and Lund, J. S., 1995, Connections between the pulvinar complex and cytochrome oxidase-defined compartments in visual area V2 of macaque monkey, *Exp. Brain Res.* **104:**419–430.

Livingstone, M. S., and D. H., 1984, Anatomy and physiology of a color system in the primate visual cortex, *J. Neurosci.* **4:**309–356.

Livingstone, M. S., and Hubel, D. H., 1987a, Connections between layer 4B of area 17 and the thick cytochrome oxidase stripes of area 18 in the squirrel monkey, *J. Neurosci.* **7:**3371–3377.

Livingstone, M. S., and Hubel, D. H., 1987b, Psychophysical evidence for separate channels for the perception of form, color, and movement, and depth, *J. Neurosci.* **7:**3416–3468.

Livingstone, M., and Hubel, D., 1988, Segregation of form, color, movement, and depth: Anatomy, physiology, and perception, *Science* **240:**740–749.

Lund, J. S., Hendrikson, A. E., Ogren, M. P., and Tobin, E. A., 1981, Anatomical organization of primate visual cortical area V2, *J. Comp. Neurol.* **202:**19–45.

Malach, R., Amir, Y., Harel, M., and Grinvald, A., 1993, Relationship between intrinsic connections and functional architecture revealed by optical imaging and *in-vitro* targeted biocytin injections in primate striate cortex, *Proc. Natl. Acad. Sci. USA* **90:**10469–10473.

Malach, R., Tootell, R. B. H., and Malonek, D., 1994, Relationship between orientation domains, cytochrome oxidase stripes, and intrinsic horizontal connections in squirrel monkey area V2, *Cerebral Cortex* **4:**151–165.

Maunsell, J. H. R., and Gibson, J. R., 1992, Visual response latencies in striate cortex of the macaque monkey, *J. Neurophysiol.* **68:**1332–1344.

Maunsell, J. H. R., and Van Essen, D. C., 1983, The connections of the middle temporal visual area (MT) in the macaque monkey, *J. Neurosci.* **3:**2563–2586.

Maunsell, J. H. R., Nealy, T. A., and Depriest, D. D., 1991, Magnocellular and parvocellular contributions to responses in the middle temporal visual area (MT) of the macaque monkey, *J. Neurosci.* **10:**3323–3334.

Merigan, W. H., 1989, Chromatic and achromatic vision of macaques: Role of the P pathway, *J. Neurosci.* **9:**776–783.

Merigan, W. H., Maunsell, J. H. R., 1993, How parallel are the visual pathways? *Annu. Rev. Neurosci.* **16:**369–402.

Merigan, W. H., Nealey, T. A., and Maunsell, J. H. R., 1993, The effects of lesions of cortical area V2 in macaques, *J. Neurosci.* **13:**3180–3191.

Mignard, M., and Malpeli, J. G., 1991, Paths of information flow through visual cortex, *Science* **251:**1249–1251.

Morgan, M. J., and Aiba, T. S., 1985, Positional acuity with chromatic stimuli, *Vision Res.* **25:**689–695.

Munk, M. H. J., Nowak, L. G., Girard, P., Chounlamountri, N., and Bullier, J., 1995, Visual latencies in cytochrome oxidase bands of macaque area V2, *Proc. Natl. Acad. Sci. USA* **92:**988–992.

Nakamura, H., Gattass, R., Desimone, R., and Ungerleider, L. G., 1993, The modular organization of projections from areas V1 and V2 to areas V4 and TEO in macaques, *J. Neurosci.* **13:**3681–3691.

Nealey, T. A., Ferrera, V. P., Maunsell, J. H. R., 1991, Magnocellular and parvocellular contributions to the ventral extrastriate cortical processing stream, *Soc. Neurosci. Abstr.* **17:**525.

Nelson, J. I., Salin, P. A., Munk, H. J., Arzi, M., and Bullier, J., 1992, Spatial and temporal coherence in cortico-cortical connections: A cross correlation study in areas 17 and 18 in the cat, *Visual Neurosci.* **9:**21–37.

Nowak, L. G., Munk, M. H. J., Girard, P., and Bullier, J., 1995a, Visual latencies in areas V1 and V2 of the macaque monkey, *Visual Neurosci.* **12:**371–384.

Nowak, L. G., Munk, M. H. J., Nelson, J. I., James, A. C., and Buller, J., 1995b, The structural basis of cortical synchronization. I. Three types of interhemispheric coupling, *J. Neurophysiol.* **74:**2379–2400.

Ogren, M. P., and Hendrickson, A. E., 1977, The distribution of pulvinar terminals in visual areas 17 and 18 of the monkey, *Brain Res.* **137:**343–350.

Peterhans, E., and von der Heydt, R., 1989, Mechanisms of contour perception in monkey visual cortex. II. Contours bridging gaps, *J. Neurosci.* **9:**1749–1763.

Peterhans, E., and von der Heydt, R., 1993, Functional organization of area V2 in the alert macaque, *Eur. J. Neurosci.* **5:**509–524.

Poggio, G. F., and Fischer, B., 1977, Binocular interaction and depth sensitivity in striate and prestriate cortex of behaving rhesus monkey, *J. Neurophysiol.* **40:**1392–1405.

Raiguel, S. E., Lagae, L., Bulyas, B., and Orban, G. A., 1989, Response latencies of visual cells in macaque areas V1, V2, and V5, *Brain Res.* **493:**155–159.

Rockland, K. S., 1985, A reticular pattern of intrinsic connections in primate area V2 (area 18), *J. Comp. Neurol.* **235:**467–478.

Rockland, K. S., 1992, Laminar distribution of neurons projecting from area V1 to V2 in macaque and squirrel monkeys, *Cerebral Cortex* **2:**38–47.

Rockland, K. S., and Pandya, D. N., 1979, Laminar origins and terminations of cortical connections to the occipital lobe in the rhesus monkey, *Brain Res.* **179:**3–20.

Rockland, K. S., and Virga, A., 1989, Terminal arbors of individual "feedback" axons projecting from area V2 to V1 in the macaque monkey: A study using immunohistochemistry of anterogradely transported *Phaseolus vulgaris*-leucoagglutinin, *J. Comp. Neurol.* **285:**54–72.

Rockland, K. S., and Virga, A., 1990, Organization of individual cortical axons projecting from area V1 (area 17) to V2 (area 18) in the macaque monkey, *Visual Neurosci.* **4:**11–28.

Rockland, K. S., Saleem, K. S., and Tanaka, K., 1994, Divergent feedback connections from areas V4 and TEO in the macaque, *Visual Neurosci.* **11:**579–600.

Roe, A. W., and Ts'o, D. Y., 1992, Functional connectivity between V1 and V2 in the primate, *Soc. Neurosci. Abstr.* **18:**11.

Roe, A. W., and Ts'o, D. Y., 1994, Relationships between topographic maps in V1 and V2 revealed by optical imaging with spot stimuli, *Soc. Neurosci. Abstr.* **20:**840.

Roe, A. W., and Ts'o, D. Y., 1995, Visual topography in primate V2: Multiple representation across functional stripes, *J. Neurosci.* **15:**3689–3715.

Roe, A. W., and Ts'o, D. Y., 1997, Functional connectivity between primate V1 and V2, submitted.

Rosa, M. G. P., Sousa, A. P. B., and Gatass, R., 1988, Representation of the visual field in the second visual area in the *Cebus* monkey, *J. Comp. Neurol.* **275:**326–345.

Sakitt, B., 1982, Why the cortical magnification factor in rhesus cannot be isotropic, *Vision Res.* **22:**417–421.

Sandell, J. H., and Schiller, P. H., 1982, Effect of cooling area 18 on striate cortex cells in the squirrel monkey, *J. Neurophysiol.* **48:**38–48.

Schiller, P. H., and Malpeli, G. J., 1977, The effect of cooling area 18 on striate cortex cells in the squirrel monkey, *Brain Res.* **126:**366–369.

Schiller, P. H., Logothetis, N. K., and Charles, E. R., 1990, Role of the color-opponent and broad-band channels in vision, *Visual Neurosci.* **5:**321–346.

Sereno, M. I., McDonald, C. T., and Allman, J. M., 1994, Analysis of retinotopic maps in extrastriate cortex, *Cerebral Cortex* **4:**601–620.

Sereno, M. I., Dale, A. M., Repas, J. B., Lwong, K. K., Belliveau, J. W., Brady, T. J., Rosen, B. R., and Tootell, R. B. H., 1995, Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging, *Science* **268:**889–893.

Shapley, R., 1990, Visual sensitivity and parallel retinocortical channels, *Annu. Rev. Psychol.* **41:**635–658.

Shipp, S., and Zeki, S., 1985, Segregation of pathways leading from area V2 to areas V4 and V5 of macaque monkey, *Nature* **315:**322–325.

Shipp, S., and Zeki, S., 1989, The organization of connections between areas V5 and V2 in macaque monkey visual cortex, *Eur. J. Neurosci.* **1:**333–354.

Spatz, W. B., Tigges, J., and Tigges, M., 1970, Subcortical projections, cortical associations, and some intrinsic laminar connections of the striate cortex in the squirrel monkey (Saimiri), *J. Comp. Neurol.* **140:**155–174.

Talbot, S. A., and Marshall, W. H., 1941, Physiological studies on neural mechanisms of visual localization and discrimination, *Am. J. Opthalmol.* **24:**1255–1263.

Tigges, J., Tigges, M., Anschel, S., Cross, N. A., Letbetter, W. D., and McBride, R. L., 1981, Areal and laminar distribution of neurons interconnecting the central visual cortical areas 17, 18, 19, and MT in the squirrel monkey (Saimiri), *J. Comp. Neurol.* **202:**539–560.

Tootell, R. B. H., Silverman, M. S., De Valois, R. L., and Jacobs, G. H., 1983, Functional organization of the second cortical visual area in primates, *Science* **220:**737–739.

Tootell, R. B. H., and Hamilton, S. L., 1989, Functional anatomy of the second visual area (V2) in the macaque, *J. Neurosci.* **9:**2620–2644.

Tootell, R. B. H., Switkes, E., Silverman, M. S., and Hamilton, S. L., 1988a, Functional anatomy of macaque striate cortex. II. Retinotopic organization, *J. Neurosci.* **8:**1531–1568.

Tootell, R. B. H., Silverman, M. S., Hamilton, S. L., DeValois, R. L., and Switkes, E., 1988b, Functional anatomy of macaque striate cortex. III. Color, *J. Neurosci.* **8:**1569–1593.

Tootell, R. B. H., Reppas, J. B., Kwong, K. K., Malach, R., Born, R. T., Brady, T. J., Rosen, B. R., and Belliveau, J. W., 1995, Functional analysis of human MT and related visual cortical areas using magnetic resonance imaging, *J. Neurosci.* **15:**3215–3230.

Ts'o, D. Y., and Gilbert, C. D., 1988, The organization of chromatic and spatial interactions in the primate striate cortex, *J. Neurosci.* **8:**1712–1727.

Ts'o, D. Y., Gilbert, C. D., and Wiesel, T. N., 1986, Relationships between horizontal interactions and functional architecture in the cat striate cortex as revealed by cross-correlation analysis, *J. Neurosci.* **6:**1160–1170.

Ts'o, D. Y., Frostig, R. D., Lieke, E. E., and Grinvald, A., 1990a, Functional organization of primate visual cortex revealed by high resolution optical imaging, *Science* **249:**417–420.

Ts'o, D. Y., Gilbert, C. D., and Wiesel, T. N., 1990b, Functional architecture of color and disparity in visual area 2 of macaque monkey, *Soc. Neurosci. Abstr.* **16:**293.

Ts'o, D. Y., Gilbert, C. D., and Wiesel, T. N., 1991, Orientation selectivity of and interactions between color and disparity subcompartments in area V2 of macaque monkey, *Soc. Neurosci. Abstr.* **17:**1089.

Ts'o, D. Y., Roe, A. W., and Shey, J., 1993, Functional connectivity within V1 and V2: Patterns and dynamics, *Soc. Neurosci. Abstr.* **19:**1499.

Ts'o, D. Y., Gilbert, C. D., and Roe, A. W., 1997, Functional architecture of color and disparity processing in primate visual area 2, submitted.

Vaina, L. M., Lemay, M., Bienfang, D. C., Choi, A. Y., and Nakayama, K., 1990, Intact "biological motion" and "structure from motion" perception in a patient with impaired motion mechanisms: A case study, *Visual Neurosci.* **5:**353–369.

Valverde, F., 1985, The organizing principles of the primary visual cortex in the monkey, in: *Cerebral Cortex,* Volume 3, *Visual Cortex* (E. G., Jones, and A. A. Peters, eds.), Plenum Press, New York, pp. 207–257.

Van Essen, D. C., 1985, Functional organization of primate visual cortex, in: *Cerebral Cortex,* Volume 3, *Visual Cortex* (E. G., Jones, and A. A. Peters, eds.), Plenum Press, New York, pp. 259–329.

Van Essen, D. C., and Zeki, S. M., 1978, The topographic organization of rhesus monkey prestriate cortex, *J. Physiol.* (Lond.) **277:**193–226.

Van Essen, D. C., and Maunsell, J. H. R., 1983, Hierarchical organization and functional streams in the visual cortex, *Trends Neurosci.* **6:**370–375.

Van Essen, D. C., Newsome, W. T., and Maunsell, J. H. R., 1984, The visual field representation in striate cortex of the macaque monkey: Asymmetries, anisotropies, and individual variability, *Vision Res.* **24:**429–448.

Van Essen, D. C., Newsome, W. T., Maunsell, J. H. R., and 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, *J. Comp. Neurol.* **244:**451–480.

Von der Heydt, R., and Peterhans, E., 1989, Mechanisms of contour perception in monkey visual cortex. I. Lines of pattern discontinuity, *J. Neurosci.* **9:**1731–1748.

Weller, R. E., and Kaas, J. H., 1983, Retinotopic patterns of connections of area 17 with visual areas V-II and MT in macaque monkeys, *J. Comp. Neurol.* **220:**253–279.

Wiesel, T. N., and Hubel, D. H., 1966, Spatial and chromatic interactions in the lateral geniculate body of the rhesus monkey, *J. Neurophys.* **29:**1115–1156.

Wong-Riley, M. T. T., 1979a, Changes in the visual system of monocularly sutured or enucleated cats demonstrable with cytochrome oxidase histochemistry, *Brain Res.* **171:**11–28.

Wong-Riley, M. T. T., 1979b, Columnar cortico-cortical interconnections within the visual system of the squirrel and macaque monkeys, *Brain Res.* **162:**201–217.

Wong-Riley, M. T. T., Hevner, R. F., Cutlan, R., Earnest, M., Egan, R., Frost, J., and Nguyen, T., 1993, Cytochrome oxidase in the human visual cortex: Distribution in the developing and the adult brain, *Visual Neurosci.* **10:**41–58.

Zeki, S., 1969, The secondary visual cortex of the monkey, *Brain Res.* **13:**197–226.

Zeki, S., 1990, Functional specialization in the visual cortex: The generation of separate constructs and their multistage integration, in: *Signal and Sense: Local and Global Order in Perceptual Maps* (G. M. Edelman, W. E. Gall, and W. M. Cowan, eds.), Wiley-Liss, New York, pp. 85–130.

Zeki, S., and Shipp, S., 1987, Functional segregation within area V2 of macaque monkey visual cortex, in: *Seeing Contour and Color* (J. J. Kulikowski, C. M. Dickinson, and I. J. Murray, eds.), Pergamon Press, Oxford, pp. 120–124.

Zeki, S., Watson, J. D. G., Lueck, C. J., Friston, K. J., Kennard, C., and Frackowiak, R. S. J., 1991, A direct demonstration of functional specialization in human visual cortex, *J. Neurosci.* **11:**641–649.