Functional Compartments in Visual Cortex: Segregation and Interaction

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ABSTRACT Our understanding of the neural mechanisms underlying visual processing has been greatly advanced by the study of how neurons are organized in the visual cortex according to functional properties. The functional organizations of visual areas V1 and V2 are very distinct and highly suggestive of a visual processing architecture. Cells tuned for particular contour orientations, wavelength, retinal disparities, and other properties are clustered in different subcompartments within V1 and V2. These subcompartments are not entirely segregated from one another but interact, producing more elaborate receptive field types. We will examine how these functional domains cooperate to analyze the visual world in terms of a variety of parameters.

One of the most striking features of the primate visual cortex is the high degree of organization based on functional properties. Cells found in the visual cortex are selective for specific aspects of visual stimuli, including orientation, movement, depth, and color. Our understanding of visual processing has been greatly advanced by the study of the organization of these properties. In particular, the classical studies of Hubel and Wiesel (1968, 1974, 1977) established the columnar organization of such properties as ocular dominance and orientation selectivity and helped formulate a modular description of the organization of visual cortex. One fundamental demonstration arising from these studies is the interlacing of several functional maps (e.g., ocular dominance and orientation) within the same cortical structure. This arrangement neatly facilitates the processing of multiple dimensions for a given region in visual space.

More recent studies have further elaborated on the functional architecture of primary visual cortex (V1) as well as of extrastriate visual areas. An important discovery was the patchy staining of visual cortex for the mitochondrial enzyme cytochrome oxidase (Wong-Riley, 1979). In V1, this staining procedure, in tangential section, reveals a lattice of oval patches or blobs that physiological studies suggest are involved in color processing (figure 20.1). In other visual areas, cytochrome oxidase histology shows very different staining patterns. For example, in V2, instead of blobs, one sees a series of darkly stained bands or stripes (see figure 20.1). Electrophysiological studies show that these stripes contain clusters of cells selective for color or disparity. These and other lines of evidence indicate that although each visual area is highly organized, the specific properties that are organized and the geometry of the organization are different from area to area. Furthermore, response properties that are well organized (e.g., retinotopy, ocular dominance, and orientation in V1) in earlier cortical stages often become less well or not at all organized in higher areas (e.g., V4, MT). In contrast, other properties, though present at early stages (e.g., disparity or directionality in V1) are not well organized until higher areas (table 20.1). This observation suggests that there may be some theoretical or developmental limit on the number of properties that can be organized in the cortical structure. Most importantly, this shifting of the organizing factors from area to area further reinforces the notion that the properties that are well organized in an area indicate or even dictate the role of that area in visual processing.

In this chapter, we will discuss the functional properties of cells in visual areas V1 and V2, as well as the organizations that they form. In addition, we will examine the segregation between the different functional compartments and the degree to which these compartments interact.
Functional properties and organization in V1

Physiological studies in V1 have found a wide range of response properties, several of which have been demonstrated to be systematically represented. In addition to a precise retinotopy, V1 was found to contain a pronounced columnar organization for ocular dominance and orientation (see color plate 5). Also introduced by the classical work of Hubel and Wiesel was the notion of a hypercolumn, a complete set of columns of one type, representing, for example, all orientations, arranged in an orderly manner. Interwoven with the columns of one functional property are the columns of other functional properties, such that a complete set of hypercolumns for all properties form the basic module of cortical organization required to process a given region in visual space. Based on electrophysiological studies, the original "icecube model" of Hubel and Wiesel (1977) depicted an orthogonal arrangement of ocular dominance and orientation hypercolumns (figure 20.2).

This model of cortical organization has been examined more recently with optical imaging methods. Two such studies (Bartfeld and Grinvald, 1992; Blasdel, 1992a, b) found that the orientation columns do run perpendicularly to the ocular dominance columns at the ocular dominance borders. Orientation selectivity, then, changes smoothly and regularly at the ocular dominance borders, as in the original icecube model. However, the orientation changes can become more

Table 20.1

<table>
<thead>
<tr>
<th>Functional Property</th>
<th>V1</th>
<th>V2</th>
<th>V4</th>
<th>MT</th>
</tr>
</thead>
<tbody>
<tr>
<td>Retinotopy</td>
<td>Yes</td>
<td>Yes, multiple maps</td>
<td>Degraded</td>
<td>Degraded</td>
</tr>
<tr>
<td>Ocular dominance</td>
<td>Yes</td>
<td>No</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td>Orientation</td>
<td>Yes</td>
<td>Yes, in some regions</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Color</td>
<td>Yes, blobs and bridges</td>
<td>Yes, color stripes</td>
<td>Yes?</td>
<td>No</td>
</tr>
<tr>
<td>Directionality</td>
<td>No?</td>
<td>No?</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Disparity</td>
<td>No</td>
<td>Yes, disparity stripes</td>
<td>No?</td>
<td>Yes?</td>
</tr>
<tr>
<td>End-inhibition</td>
<td>No</td>
<td>Yes?</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: As can be seen, though cells with a given property may exist within an area, those cells may or may not be organized. What properties are organized within a given area changes from one to the next: Properties that in previous areas (areas lower in the hierarchy) are well organized may become less well organized, whereas other properties previously not organized, though present, become organized.
However, several blob color cell types did not correspond to LGN types. One prominent example were cells described as double-color-opponent, having spatially opponent fields with color opponency in both center and surround. Subsequent studies (Ts’o and Gilbert, 1988) showed that the majority of these cells did not have true double-color-opponent properties (Daw, 1968), as their surround was always suppressive and the response to stationary isoluminant color contrast was poor. Accordingly, this class of color cell was named *modified type II*, suggesting that the suppressive surround represents a modification of the LGN type II field. Color, then, is yet another functional dimension that is integrated into the cortical matrix. These data have prompted a revision of the iccecube model that incorporates the blobs into the centers of each ocular dominance column (Livingstone and Hubel, 1984a) (see figure 20.2).

**Color opponency–specific blobs** The view of the organization of the blob color system has been further refined by the finding that the blobs are color opponency–specific. In addition to confirming (at least in the superficial cortical layers) a patchy or columnar organization of color in V1 (see also Gouras, 1974; Michael, 1981), Ts’o and Gilbert (1988) reported that single vertical electrode penetrations within blobs encounter color cells of only one color opponency, either red versus green or blue versus yellow (see also Dow and Vautin, 1987). Furthermore, cells recorded in neighboring vertical penetrations within a single blob share the same color opponency. These findings suggest that individual blobs are dedicated to the processing of one color opponency system. Some blobs were found that did not contain any color cells but contained only broad-band center-surround (type III) cells. This finding may be relevant in interpreting the role of the blobs in nocturnal primates, such as the owl monkey, that have very poor color vision.

The color-specific blobs across cortex do not share equal representation in V1. Based on multiple electrode penetrations into the perifoveal cortical representation of V1, Ts’o and Gilbert (1988) found a 3:1 ratio of red/green to blue/yellow blobs, paralleling biases found in the retina (5:2) (see Gouras, 1968; DeMonasterio and Gouras, 1975; Schiller and Malpeli, 1978) and the LGN (12:1) (see Wiesel and Hubel, 1966; Dreher, Fukada, and Rodieck, 1976; Kruger,
Furthermore, blue-yellow blobs seem to cluster together, suggesting a nonuniform or patchy distribution of blue cone inputs to cortex.

**Bridges** An intriguing observation first made by Horton (1984) is that the ocular dominance columns often seem paired such that the blobs of a given left-eye dominance band are connected by bridges to the blobs of only one neighboring right-eye dominance band and not the other (Figure 20.3). This pattern of pairing gives the appearance, in cytochrome oxidase histology, of railroad tracks or ladders, with the bridges appearing as ties or rungs crossing two ocular dominance bands (the rails of the track). Horton speculated that the origins of this arrangement may be tied to a gradual separation of the ocular dominance columns during development.

Recordings in the bridges suggest that they, like the blobs, also contain unoriented cells that are often color-selective (Ts’o and Gilbert, 1988; Landisman and Ts’o, 1992). Thus, the bridges are apparently an additional component of the V1 color system. Binocular, unoriented, color-selective cells were found in bridges between blobs of opposite ocular dominance. This view has been confirmed by optical imaging studies designed to reveal the color-selective regions of cortex (Landisman, Grinvald, and Ts’o, 1991; Landisman and Ts’o, 1992) that directly show that the bridge regions are color-selective. Bridges have also been found spanning neighboring blobs of different color opponency. Color response properties in such bridges are often found to be neither red/green nor blue/yellow but mixed in spectral selectivity.

Interposed between the interblob and the blob regions are the so-called periblob regions, in which color-oriented cells are often found (Dow and Vautin, 1987; Ts’o and Gilbert, 1988). Some initial studies using cross-correlation analysis indicate that color-oriented cells receive input from color blob cells having matching color specificity (Ts’o and Gilbert, 1988). The distribution and receptive field properties of color-oriented cells and preliminary cross-correlation data all suggest that these cells represent an interplay between the blob and interblob regions or, alternatively, between the form and color pathways.

It should be noted that other investigators using different methods of color stimulation and classification have reported little or no correlation between the presence of color-selective cells and the blobs (Lennie, Krauskopf, and Sclar, 1990; Leventhal, Thompson, and Liu, 1993). One possible difference may be the means for localizing the blobs and the consideration of the presence of the bridge regions that also contain color-selective cells. The reconciliation of these disparate views must await future studies.

**Other receptive field types** Many other receptive field properties have been described in physiological studies.
of V1. However, of these, few have been demonstrated to be systematically organized within V1. Several properties clearly have a laminar rather than columnar distribution, such as the directional cells of layer IVB (Hawken, Parker, and Lund, 1988) or the distribution of simple versus complex cells (Gilbert, 1977). No clear organization in V1 for properties such as disparity or end inhibition has yet been described.

**Horizontal Interactions Between Columnar Compartments** The vertical or interlaminar cortical connections are believed to underlie the basic columnar organization of visual cortex. The early Golgi studies that demonstrated these vertical connections (Lorenz de No, 1949) did not hint at the long lateral extent of axonal arbor present in the cortex. Evidence for the long-range horizontal connections in the cortex was first seen in degeneration studies and later in extracellular injections of tracers into primary visual cortex. Patchy patterns of label were seen to extend up to several millimeters from the injection site (Rockland and Lund, 1983; Livingstone and Hubel, 1984b; Gilbert and Wiesel, 1989). The clustered or patchy distribution of these connections, as well as their strong asymmetricities, perhaps most clearly shown in intracellular HRP studies (Gilbert and Wiesel, 1979, 1983; Martin and Whitteridge, 1984), suggested a relationship with the underlying functional architecture. This relationship was studied physiologically using the cross-correlation technique (Ts’o, Gilbert, and Wiesel, 1986), discussed in the next section. The combination of extracellular tracer injections with stains for other functional markers (such as cytochrome oxidase or 2-deoxyglucose) provided further indications that these lateral connections were specific to the functional organization. For example, a given orientation column characterized by single-unit recordings was found to receive input in a lattice-like arrangement from regions of similar orientation specificity (as revealed by 2-deoxyglucose labeling) and avoid regions of orthogonal orientation preference (Gilbert and Wiesel, 1989). In the V1 blob system, focal injections into single cytochrome oxidase blobs in layers II and III label preferentially nearby blobs up to a millimeter away, whereas injections into interblob regions label interblob regions (Livingstone and Hubel, 1984b). In contrast to the axon arborization, the functional specificity of dendritic arborizations (at least of blob cells) may be less strict (Hubener and Bolz, 1992; Malach, 1992).

**Cross-correlation studies of V1 intrinsic connectivity** The degree of functional specificity in horizontal dimension also has been investigated with physiological methods. The method of cross-correlation analysis provides a statistic measure of the temporal relationship between the firing of two cells and therefore an indication of the connectivity or interactions between the two cells. Cross-correlation studies reveal that horizontal interactions in both cat (Ts’o, Gilbert, and Wiesel, 1986; Hata et al., 1991) and monkey (Ts’o and Gilbert, 1988; Schwarz and Bolz, 1991) occur preferentially between cells of similar orientation selectivity (figure 20.4), even those with receptive fields separated by as much as 3°. Although some excitatory monosynaptic interactions were observed, common input interactions were most prevalent (40–50%). This prevalence of common input might be expected given the small synaptic efficacies involved and the high degree of interconnectivity in the cortical network.

**Connectivity of color processing** Because the blob regions represent a major component of the functional and cytoarchitectonic organization of the monkey striate cortex, it is natural to ask how the blobs might interact with the nonblob regions. Livingstone and Hubel (1984b), using focal extracellular injections of HRP, demonstrated cross-correlation between adjacent blobs and also between neighboring nonblob (interblob) regions. No connections between blob and interblob regions were found. This segregation of connections was confirmed and extended with results using cross-correlation analysis, which showed that blob-blob connections existed between cells with matching color opponency (figure 20.5) and that interblob-interblob connections existed between cells with matching orientation preference (Ts’o and Gilbert, 1988). Preliminary anatomical results, using focal injections at blob sites whose color opponent had been previously determined, seem to support this arrangement (Ts’o, 1989). Cross-correlation studies have also shown that lateral connections contribute to the construction of specific colorreceptive field properties. For example, type II cells (cells with color-opponent centers but no surrounds) provide monosynaptic input to modified type II cells (cells with color-opponent centers and broadband surrounds) and type I cells (basic center-surround color cells) and modified type II cells contribute directly to oriented color cells in V1 (Ts’o and Gilbert, 1988). These findings suggest that lateral connections within
Correlograms obtained from two cell pairs. (A) The cell pair had similar receptive properties: The first cell had an orientation preference of 120°, directional preference to the right, and an ocular dominance group of 2; the second cell had identical orientation and direction preference and an ocular dominance group of 3. (B) The first cell here was the same as the first cell in (A). The second cell had different receptive field properties: an orientation preference of 20°, upward directionality, and an ocular dominance of 5.

(Left) Blue-ON yellow-OFF type I to type III OFF-center correlogram. (Right) Blue-ON yellow-OFF type I to Blue-ON yellow-OFF type I cell. Correlograms were normalized by the baseline correlation. The shape and pattern of the peak indicates an excitatory monosynaptic connection from one type I to the other. $N_s = 4378; N_b = 19,370$; contribution, 13.2%; effectiveness, 3.0%. W (white) indicates broadband spectral properties.
the cortex have a like-to-like pattern, within both the orientation domain (figure 20.6) and the color domain. Undoubtedly, similar rules of connectivity may be found within other functional groupings.

Initial studies have shown that many of these cortical patterns of cross-correlation are not static but rather change their strength and signature with changes in state or stimulus context (figure 20.7). This type of finding, which also has been observed in the cortico-cortical interactions between V1 and V2 (Ts' o, Roe, and Shey, 1993) as well as in other cortical areas (Aersten et al., 1991; Ahissar et al., 1992), emphasizes the dynamic nature of cortical processing. However, attaining an understanding of the origins of such changes remains challenging.

**Functional properties and functional organization in V2**

**Inputs to V2** Unlike the visual system in the cat, the second visual area (V2) in the primate receives its visual inputs primarily from V1. Direct geniculate
input to V2 is sparse and scattered and arises from the interlaminar zones and the S layers of the LGN (Bullier and Kennedy, 1983). Reversible inactivation of V1 by cortical cooling renders cells in V2 visually unresponsive (Schiller and Malpeli, 1977; Girard and Bullier, 1989), suggesting that V1 is the primary source of visual drive for V2.

**Stripes in V2** In contrast to V1, cytochrome oxidase staining in the second visual area, V2, reveals a pattern of bands or stripes of dense labeling, separated by pale interstripes (Livingstone and Hubel, 1982, 1984a; Humphrey and Hendrickson, 1983; Tootell et al., 1983; Horton, 1984; DeYoe and Van Essen, 1985; Shipp and Zeki, 1985). The V2 stripes are functionally distinct and contain different populations of functional cell types. In contrast to V1, there is no apparent organization to ocular dominance in V2 and most V2 cells are binocularly responsive. Cells in the thin stripes are color-selective, some of which are similar to the modified type II cells seen in V1. Interstripe regions are characterized by oriented, non-color-selective fields that commonly exhibit end-stopping. Thick-stripe cells usually are oriented, lack end-stopping, and often are disparity-sensitive (DeYoe and Van Essen, 1985; Hubel and Livingstone, 1987; Ts’o, Gilbert, and Wiesel, 1990). In addition to these physiological findings, the pattern of V2 corticocortical connections seen in anatomical tracer studies suggests that thin, pale, and thick stripes are the V2 components of the color, form, and motion-disparity pathways, respectively (see Van Essen and DeYoe, this volume). Some reports, however, suggest a less clear-cut relationship between V2 cell properties and the V2 stripe organization. Studies using achromatic and isoluminant chromatic gratings to characterize V2 cells quantitatively have found a less striking segregation of cell types (Levitt and Movshon, 1990). These differences in findings may be related to differences in the methods of cell classification or approaches to correlating physiology with anatomy.

**Stripe substructure** Within a single stripe in V2, there is some evidence to indicate clustering of cell properties such as color, disparity, and orientation (DeYoe and Van Essen, 1985; Tootell and Hamilton, 1989; Ts’o et al., 1989). Other functional methods used to image stripe organization, such as 2-deoxyglucose labeling (Tootell et al., 1983; Tootell and Hamilton, 1989) and optical imaging of intrinsic signals (Ts’o et al., 1990; Ts’o, Gilbert, and Wiesel, 1990; Ts’o, Roe, and Shey, 1993) clearly indicate clustering of functional activity along the length of the stripes. In thin stripes, for example, physiological recordings encounter patches of red-green opponent-dominated patches as well as blue-yellow-dominated patches. Disparity-tuned thick-stripe cells, as mentioned previously, tend to fall into near cell-dominated, far cell-dominated, tuned excitatory, and tuned inhibitory clusters (Ts’o, Gilbert, and Wiesel, 1990, 1991). In pale stripes, physiological recordings frequently encounter a cluster of similarly oriented cells adjacent to another cluster of oriented cells selective for a very different orientation. It is clear that V2 stripes are, in fact, not homogeneous structures but rather collections of distinct functional modules (see color plate 6).

**Higher-order receptive field types in V2** Several types of higher-order receptive fields have been described in V2. Two types of color cells are the spot cell and the oriented color cell. Spot cells (Baizer, Robinson, and Dow, 1977; Hubel and Livingstone, 1987) are unoriented color-selective cells that respond optimally to a small spot. However, unlike a standard center-surround cell, the spot cell has a spatial independence such that a small spot (e.g., 0.25°) is effective over a relatively large portion (e.g., 4 x 4°) of the visual field (Hubel and Livingstone, 1985, 1987). These spot cells are not found in V1 and may represent a further elaboration in V2 of the modified type II cells of V1. One possible circuit would involve convergence from modified type II cells with matching color opponency and both eye dominances and with receptive field centers scattered over the large area corresponding to the spot cell’s field (typically four to eight times larger than a modified type II cell at the same eccentricity). Such convergence would require input either intrinsically from the modified type II cells within V2 or via corticocortical connections from V1-modified type II cells over a relatively wide area of cortex.

Although it is still unclear how oriented color cells are organized in either V1 or V2, preliminary evidence suggests that in V1 they are localized in the border regions between the color-selective blobs and the orientation-selective interblobs (Ts’o and Gilbert, 1988). In V2, they are similarly located at such border zones (i.e., thin, pale borders). It is possible that oriented color cells in V2 receive input directly from oriented color cells in V1 (and thus comprise a separate
oriented color cell pathway) or, alternatively, they may be constructed de novo via convergent input from unoriented color cells in V1 or V2 (Roe and Ts’o, 1992).

An organization apparently absent in V1 that is prominent in V2 is the organization for disparity. Disparity cells, defined by their selectivity for stimuli presented at a specific retinal disparity, are common to the thick stripes of V2. Most remarkable is the predominance of obligatory binocular cells, disparity cells that respond vigorously to stimulation of both eyes when stimuli are present at the optimal disparity but are absolutely silent to monocular stimulation of any type. Studies describing near cells (crossed disparity) and far cells (uncrossed disparity) in V2 suggest a possible clustered organization of near cells and far cells in the V2 thick stripes (Ts’o, Gilbert, and Wiesel, 1990, 1991). Another example of a mixed-property cell occurring at a stripe border region is the color-disparity cell. Seen in both cytochrome oxidase–stained sections and in optical images of functional organization in V2 are the regions where thick and thin stripes appear to merge, resulting in the absence of an intervening pale stripe. These color-disparity borders often are characterized by patches of color-disparity cells and may result from the convergence of the two functional compartments (Ts’o, Gilbert, and Wiesel, 1990, 1991).

Form processing also gains in complexity in V2. Unlike standard orientation-selective cells, some V2 cells, called subjective contour cells (von der Heydt and Peterhans, 1989; Peterhans and von der Heydt, 1989), respond to stimulus patterns that are perceived to contain contours not actually present in the stimulus. These investigators proposed a model for the construction of the V2 subjective contour cell from the convergence of appropriately positioned end-inhibited cells in V1 and V2.

**Topography in V2** Yet another distinguishing feature of V2 is its retinotopic organization. It was previously known that receptive fields in V2 are larger than those in V1 and retinotopy in V2 is less precise than that in V1 (Gatass, Gross, and Sandell, 1981). With the discovery of cytochrome oxidase and the stripe organization in V2, a new issue arose concerning visuotopic mapping in V2. In V1, there is a point-to-point mapping of the visual field onto the cortex such that roughly a square millimeter of cortex, which spans a left-eye and a right-eye ocular dominance column, represents a specific locus in visual space. In V2, each thick-pale–thin-pale cycle spans approximately 4 mm of cortex. Therefore, roughly speaking, at any single iso eccentricity, each cycle of thin-pale–thick-pale stripes potentially receives input from a cortical area spanning four to five ocular dominance hypercolumns, or approximately the width of ten blobs. How does the region of visual space that is represented across several hypercolumns map onto a set of three functionally distinct stripes? Evidence from receptive fields recorded in long tangential penetrations across the stripes in V2 suggest that there is a multiple and discontinuous mapping of the visual field in V2 (Roe and Ts’o, 1993). In other words, any region of visual space is represented at least in triplicate across the thin, pale, and thick stripes in V2. An electrode traveling across any single stripe will encounter a continuous progression of receptive fields, followed by a jump back in receptive field progression at the stripe border, followed by another continuous progression representing the same region of visual space in a different functional domain. Therefore, several ocular dominance columns of V1 must map in a topographical manner onto each of the color, form, and disparity stripes across the V1/V2 border. Results from anatomical studies are consistent with this prediction (Livingstone and Hubel, 1984a).

**Connectivity, interactions, and the relationship between V1 and V2**

The previous section has described the difference in the functional organizations of V1 and V2 as well as differences in the types of receptive fields they contain. In V2, the emphasis in organization has shifted from one dominated by lower-level features (such as ocular dominance, orientation, color, and point-to-point mapping) to one concerned with more integrated features (such as disparity, contour recognition on a more global level, spatial invariance of color features, and independent topography within selected feature domains). What corticocortical connectivities underlie these transformations in functional properties and functional organization? To approach this question, we first examine the anatomical basis of V1/V2 connectivity.

**V1/V2 Anatomical Connectivity** Anatomical studies suggest the functional segregation of inputs from V1
of the blob and interblob regions in V1 (Livingstone and Hubel, 1984a) and stripes in V2 (Hubel and Livingstone, 1987) suggested a segregation of form, color, and motion-stereo processing streams. This view of visual processing has been both supported and criticized (for reviews, see Livingstone and Hubel, 1988; Schiller and Logothetis, 1990; Merigan and Maunsell, 1993).

Anatomical studies to date have demonstrated the general patterns of connectivity between the V2 stripes and other compartments in other cortical areas (see Van Essen and DeYoe, this volume). However, we know that the stripes are actually composed of a series of functionally distinct patches. It is then expected that V2 connectivity at a finer level bears some relationship to the subcompartments within a single stripe. Furthermore, it is likely the corticocortical connections play a significant role in the generation of particular higher-order receptive field properties in V2 and elsewhere. Investigation of these issues will require examining the connectivity at a finer scale, both anatomically and physiologically.

V1/V2 Functional Connectivity Cross-correlation analysis has been used to examine the patterns of V1/V2 corticocortical connectivity (Bullier, Munk, and Nowak, 1992; Roe and Ts'o, 1992), and two notable characteristics have emerged. The first concerns the degree of convergence and divergence between V1 and V2. As stated previously, each stripe in V2 is likely to receive input from as many as four to five ocular dominance hypercolumns. Thus, V1/V2 connectivity is likely to be highly convergent and divergent. Indeed, cross-correlation studies indicate a high degree of convergence and divergence in V1/V2 connectivity in comparison to V1/V1 cell pairs (Bullier, Munk, and Nowak, 1992; Roe and Ts'o, 1992). V1/V2 correlations are typically 50–200 ms wide compared to V1/V1 or V2/V2 correlation peaks, which are typically 5–20 ms wide. This amount of temporal dispersion in the correlograms found between V1 and V2 suggests a higher degree of synaptic jitter, perhaps due to a larger number of weaker synapses participating in the interaction. V1/V2 cross-correlation peaks are also often centered on zero, indicating the presence of common input. Similarly, broad and centered cross-correlations have been reported between cell pairs in cat area 17/18 (Nelson et al., 1992). Such peaks could result from common input arising in the pulvinar (Livingstone
and Hubel, 1982; Bullier and Kennedy, 1983; Horton, 1984); however, a more likely source may be a V1 cell or assembly of cells that provide inputs to both the V1 cell and the V2 cell under study. These findings also suggest that individual V1 and V2 cells participate in large corticocortical networks.

The second important aspect of V1/V2 connectivity relates to functional specificity. In V1, cross-correlation studies (Ts’o, Gilbert, and Wiesel, 1986; Hata et al., 1991) have revealed that strong correlation peaks occur between cells of similar functional specificity (e.g., similar color preference, orientation) but not between those of different functional specificity (see color plate 7). In general, V1/V2 cell pairs also exhibit this pattern of behavior (Roe and Ts’o, 1992). For example, in the color domain, color cell pairs with matched color specificities exhibit peaked correlations, whereas those with different color specificities exhibit flat correlations. Similarly, only broadband oriented cell pairs with similar orientation selectivity have peaked correlations. Receptive field overlap is an important determinant for functional interaction in some domains but not in others. Thus, interactions between V1 and V2 cells are specific not only in terms of the types and number of cells with which they interact but also in terms of the extent of cortex across which they interact.

These findings contribute to a view of corticocortical processing which extends beyond that of simply channeling information from one cortical level to another. Functional specificity, which was initially suggested by anatomical studies, actually occurs at a much more specialized level, at the level of specific functional properties such as color, orientation, and spatial location. However, this specificity is maintained despite the high degree of convergence and divergence present in V1/V2 projections. This convergent-divergent yet specific type of connectivity is consistent with the pattern of multiple and segregated topographical representation in V2. It is also likely to be important for the generation of specific cell types in V2. For example, the spot cell may summate inputs from color cells arising from a large extent of V1, all of which have the same color specificity. Similarly, the subjective contour cell may arise due to converging inputs from similarly oriented broadband cells arising from many locations in V1. Thus, corticocortical projections participate in specific functional transformations in sensory representation. These transformations determine both the mode of topographical representation in a target cortical area and the generation of specific functional properties there.

Conclusion

Visual areas V1 and V2 are segregated into functional compartments specialized for such properties as orientation, color, and disparity. However, the segregation is far from absolute, and much interaction occurs between neighboring compartments. Whether the purpose of compartmentalization is simply for developmental or anatomical convenience or for facilitating specific computations within a given functional domain or both, it is likely that the organization of multiple feature domains within a cortical area reflects the processing strategies employed and is an important clue to the role of that cortical area in visual processing.

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