Form Processing Modules in Primate Area V4

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Ghose, Geoffrey M. and Daniel Y. Ts'o. Form processing modules in primate area V4. *J. Neurophysiol.* 77: 2191–2196, 1997. Area V4 occupies a central position among the areas of the primate cerebral cortex involved with object recognition and analysis. Consistent with this role, neurons in V4 are selective for many visual attributes including color, orientation, and binocular disparity. However, it is uncertain whether cells within V4 are organized with respect to these properties. In this study we used in vivo optical imaging and electrophysiology in macaque visual cortex to show that cells that share certain physiological properties are indeed grouped together in V4. Our results revealed regions containing cells with common orientation selectivity. These regions were similar in size to those seen in V2 and much larger than those seen in V1 and were confirmed by appropriately targeted single-unit recording. Surprisingly, orientation organization visible through imaging was limited to the portion of V4 representing the central visual fields. Optical imaging also revealed a functional organization related to stimulus size. Size-sensitive regions (S regions) contained cells that were strongly suppressed by large stimuli. In contrast to V2, S regions in V4 contain orientation domains. These results suggest that V4 contains modular assemblies of cells related to particular aspects of form analysis. Such organization may contribute to the construction of object-based representations.

INTRODUCTION

There has been substantial progress in our understanding of the functional role and architecture of primary visual cortex (V1), as well as several extrastriate visual areas, including V2 and V5 (MT) (Albright 1984; Felleman and Van Essen 1991; Hubel and Livingstone 1987; Zeki and Shipp 1988). However, despite the central position of extrastriate area V4 in the pathway devoted to object analysis (Baizer et al. 1991; Tanaka et al. 1991), a definitive notion of this area's functional significance has not yet emerged. Although the initial study of V4 by Zeki (1973) suggested that the area is particularly concerned with the processing of color information, subsequent investigations have shown that V4 cells can respond selectively to other attributes including orientation, binocular disparity, and size (Cheng et al. 1994; Desimone et al. 1985; Desimone and Schein 1987; Gallant et al. 1993). A similar variety of response properties is also present in V1 and V2 and in these visual areas neurons are largely segregated into compartments of like functional type. To date, however, there have been no direct demonstrations of functional organization within V4.

METHODS

To ascertain whether such organization exists within V4, we used high-resolution optical imaging of V4 along the prelunate gyrus of anesthetized and paralyzed macaque monkeys. Eight *Macaca fascicularis* were anesthetized by continuous intravenous infusion of sufentanil citrate ($3–8\ \mu g \cdot kg^{-1} \cdot h^{-1}$), paralyzed (vercuronium bromide, $100\ \mu g \cdot kg^{-1} \cdot h^{-1}$), and artificially respirated. The level of anesthesia was continually verified by monitoring electrocardiogram and electroencephalogram. Adequate respiration was verified by monitoring expired CO_2. Craniotomies ($\sim 1\ cm^2$) centered along the lunate sulcus were made to expose portions of V1, V2, and V4. The eyes were fitted with contact lenses of appropriate refraction for the cathode ray tube (CRT) distance and converged by placing a Risley prism over one eye and aligning the monocular receptive fields of a V2 binocular cell. Receptive fields of single neurons were mapped electrophysiologically and used to appropriately position stimuli for imaging. Images of the cortical surface were acquired by a charge-coupled device array camera through a macroscope lens assembly during illumination by 630-nm light while visual stimuli were presented in a random order on a CRT placed 28.5 in. in front of the animal. To resolve the relatively small changes in reflectance (on the order of 1 part in 10,000) associated with neural activity, the images from 8 to 16 repetitions of each stimulus were summed. Because functional images were generated on-line, we were able to verify the increase in signal to noise as a function of repetition during the course of each experiment. Patterns of activation over the cortical surface were imaged with a spatial resolution of $43–71\ \mu m$ (Ts'o et al. 1990). Functional organization with respect to a particular stimulus parameter was visualized by subtracting images acquired during the presentation of complementary visual stimuli. For example, in Fig. 1, *A* and *C*, we constructed orientation maps by subtracting images acquired during the presentation of horizontally oriented gratings from images acquired during the presentation of vertically oriented gratings. Stimulus sets typically included gratings of different spatial frequencies, spatial extents, and color modulations.

RESULTS

With the use of these methods, a functional organization with respect to orientation was found in V4. Orientation-selective regions were similar in size to those found in V2 but considerably larger than those seen in V1 (V4: $0.15 \pm 0.015\ mm^2$, mean ± SE; V2: $0.13 \pm 0.015\ mm^2$; V1: $0.046 \pm 0.006\ mm^2$). The organization of these regions was verified by recording single neurons in locations targeted according to the orientation maps generated from optical imaging (Fig. 1*A*). In six of the eight animals the stimulus properties of single neurons were examined with the use of standard extracellular procedures at locations targeting according to the maps generated by imaging. A total of 76 cells was studied from 43 penetrations. Receptive fields were qualitatively evaluated for orientation, color, and length selectivity, location, and size with the use of hand-controlled bars. For 52 of these cells, orientation selectivity was quantitatively measured with the use of randomly interleaved sinusoidal gratings as stimuli. Orientation-selective neurons re-

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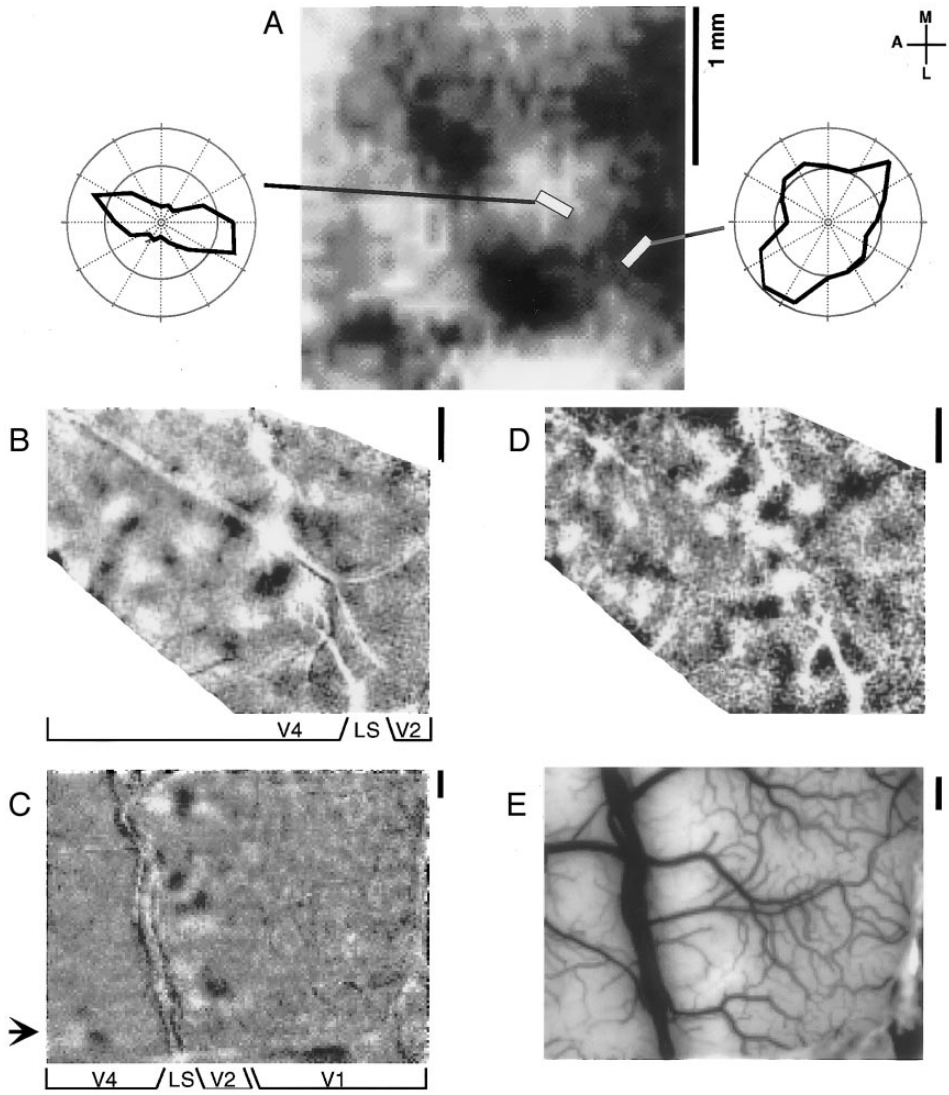

FIG. 1. Optical imaging of intrinsic reflectance changes reveals orientation domains in primary visual cortex (V1) and areas V2 and V4. Dark areas in *A* and *C*: regions preferentially responding to horizontally oriented gratings. White areas: regions preferentially responding to vertical orientations. The maximum activity-related reflectance change ($\Delta R/R$) was $\sim 3-4 \times 10^{-4}$. The size of an isoorientation region was measured by summing the polygons constructed from full-width half-maximal lines in 20 different directions from the region's local minimum (or maximum) of reflectance. All scale bars are 1 mm, and all images are oriented with medial upward and posterior to the right (Figs. 1–3). *A*: lateral exposure of V4 reveals multiple orientation domains within the foveal representation. Mean firing rate among single cells at specific locations within the exposure is plotted in the polar plots. Radial tick marks: 10 spikes/s. *B*: dark areas, 45° orientation preference; white areas, 135° orientation preference. Large diagonal line labeled LS: artifact of the large blood vessel lying along the lunate sulcus. V4 is left (anterior) of the lunate; V2 and V1 are right (posterior) of the lunate. Orientation regions are not visible along the upper (medial) edge of V4. *C*: expanded region of *A.* Orientation domains are present throughout the area of V1 that was imaged and are limited to stripe-shaped regions within V2. V1 domains are not as clear because they are close to the optical resolution in size. V4 orientation regions are only visible along the lower (lateral) edge of the exposure corresponding to more foveal representations and are absent medially. *D*: dark areas, vertical orientation preference; white areas, horizontal orientation preference on this map of the same region as shown in *B.* Note the shift between *B* and *D* in the locations of maximal activation. *E*: image of the cortical surface corresponding to *C.* The vessel along the lunate sulcus is clearly visible. Note also that the V2/V1 border indicated by change in orientation module size in *C* corresponds with a change in surface vasculature in *E.*

corded in vertical penetrations traversing up to 1.5 mm had similar orientation preferences ($\leq 30°$), suggesting a columnar organization with respect to orientation.

Unlike V1 and V2, organization for orientation as seen by optical imaging is apparently limited to the foveal representation in V4. Figure 1, *B–E*, illustrates regions that include both V2 and V4. Figure 1, *B* and *D*, shows regions of V2 and V4 that represent visual space near the fovea. In Fig. 1*B*, orientation-selective regions are visible in most of exposed V4, but are absent in the medial portion (top) that represents parafoveal visual fields. Figure 1, *C* and *E*, shows regions that represent more eccentric visual space. Figure 1*C* illustrates organization for orientation within parafoveal V1, V2, and V4 and is an expanded view of Fig. 1*A.* Cells

recorded from the center of this V4 exposure had receptive fields ~3° diam at an eccentricity of ~5°. Orientation-selective regions (dark and light patches) are present throughout the region of V1 that was imaged. In contrast to V1, orientation selectivity in V2 is confined to specific domains that correspond to the pale and thick stripe regions revealed by cytochrome oxidase staining (Hubel and Livingstone 1987; Malach et al. 1994). In this figure, V4 orientation-selective regions are not visible except for several isoorientation regions, indicated by dark and light patches, located along the lateral edge of the exposure (*bottom left*). Because V4 is roughly retinotopically organized, this lateral edge corresponds to the representation of more foveal visual space as shown in Fig. 1, *B* and *D* (Gattass et al. 1988). Because the organization was seen over stimulus sets that included variations in attributes other than orientation, we feel that it is unlikely that the differential visibility of orientation regions is due simply to confounding stimulus parameters that preferentially activate foveal cells. For example, stimulus sets included stimuli of different sizes and spatial frequencies. Finally, visualization of orientation-selective regions is not significantly compromised by vascular artifacts in any of the areas, as can be seen by comparing Fig. 1, *C* and *E*.

We examined the locations of iso-orientation regions within V4 as a function of eccentricity for all eight animals. For one animal, possibly because of the relatively medial location of the exposure, imaging failed to reveal any iso-orientation regions within V4. Another case revealed several iso-orientation regions at ~5–7° eccentricity, but no regular mosaic of such regions. For the remaining six animals, orientation-selective regions were only seen in the lateral region of V4 within the cranial exposure, corresponding to eccentricities of ~3° or less. Patterning of orientation modules over the entire exposure was only seen for lateral craniotomies, which included cells with receptive field eccentricities in this range. For example, the maps in Fig. 1, *B* and *D*, correspond to a portion of V4 in which receptive fields were smaller (1°) and more foveal (2°) than those seen in the exposure of Fig. 1*C*. Because of the consistent location of these modules in different animals, we are confident that limited extent of V4 orientation modules is not due to variations in the number of V4 orientation regions between different animals. These orientation patterns were confirmed by subsequent anatomic reconstruction to be restricted to V4. These observations indicate that the foveal region of V4 differs from the parafoveal region in its functional architecture. A possibly related anatomic observation is the distinctive nature of the inputs to the foveal representation: it is the only region of V4 that receives direct input from V1 (Nakamura et al. 1993; Yukie and Iwai 1985) and, unlike the regions of V4 that represent eccentric visual space (>20°), it projects solely to inferotemporal cortex (Baizer et al. 1991). Thus foveal V4 may constitute a specialized subarea that conveys orientation information to the temporal pathway.

Surround suppression, in which responses are suppressed by certain stimuli extending beyond the classical excitatory receptive field, is found among many V4 cells (Desimone et al. 1985, 1993; Desimone and Schein 1987; Schein and Desimone 1990). Such cells, whose responses are selective for the presence of small stimuli, might play a fundamental role in the detection of small objects in a field of larger objects (Schiller 1993). To examine functional organization for surround effects, we compared the activation seen with a pair of small stimuli with that seen with a single large stimulus. Figure 2 shows that there are distinct subregions within V4 that preferentially respond to the smaller stimuli. We call such regions S regions. Because this was a parafoveal exposure (receptive fields were between 5 and 7° eccentricity) orientation regions were not visible. To further probe the functional properties within such regions, we recorded from single cells with the use of stimulus sets that included a variety of center-surround configurations. A total of 23 cells in four animals was quantitatively studied in this manner. Electrode penetrations in S regions consistently revealed cells that were almost completely suppressed by large stimuli. For example, in Fig. 2 we see a cell that is suppressed by large stimuli to a firing rate below spontaneous activity. Outside of S regions, cells with some degree of surround suppression could also be found, but there were also many cells that optimally responded to large stimuli (Fig. 2). Interestingly, many cells outside of S regions optimally respond when the center and surround differ in orientation or spatial frequency.

To study the visuotopic organization of V4, we used optical imaging to visualize the activation associated with a single stimulus that was spatially restricted to 1–2° in size at a foveal location in visual space. Figure 3*D* shows the portion of the cortical surface that was imaged. Figure 3*A* shows the pattern of activation that such small stimuli produced in areas V2 and V4. The region shown includes that illustrated in the orientation analysis of Fig. 1, *B* and *D*. In confirmation of a previous report, such small stimuli selectively activated stripelike regions separated by ~2 mm in V2 (Roe and Ts'o 1994). In contrast to V2, the 1° stimuli activated up to six different localized regions within V4 over an area spanning ~4 mm. This spread is consistent with observations that the retinotopic mapping is considerably less precise within V4 than it is within areas V1 and V2 (Gattass et al. 1988). The relatively wide spread activation associated with small stimuli seen in V4 is likely to reflect a progressive loss of retinotopy in higher visual areas that might ultimately result in position-invariant representations. Figure 3*B* shows S regions appearing in both V2 and V4. However, their spatial configuration is clearly different: V2 S regions, unlike those of V4, are confined to stripelike domains. Although certain vascular artifacts are visible in the functional images (Fig. 3, *D* vs. *B* and *C*), neither the iso-orientation regions nor the S regions correspond to any vascular feature. This was true for all the images examined.

Because V2 and foveal V4 display organization for both surround suppression and orientation, one natural issue is the degree of segregation between these form systems in the two areas. This can be addressed by overlaying the outlines of S regions onto orientation maps (Fig. 3*C*). Such a comparison reveals that size and orientation analyses are segregated differently in the two areas. In V2, we see that the S regions do not overlap with orientation-selective regions, indicating a correspondence between S regions and thin stripes (Hubel and Livingstone 1987). By contrast, S regions in foveal V4 are not limited to unoriented regions, and can span several orientation modules.

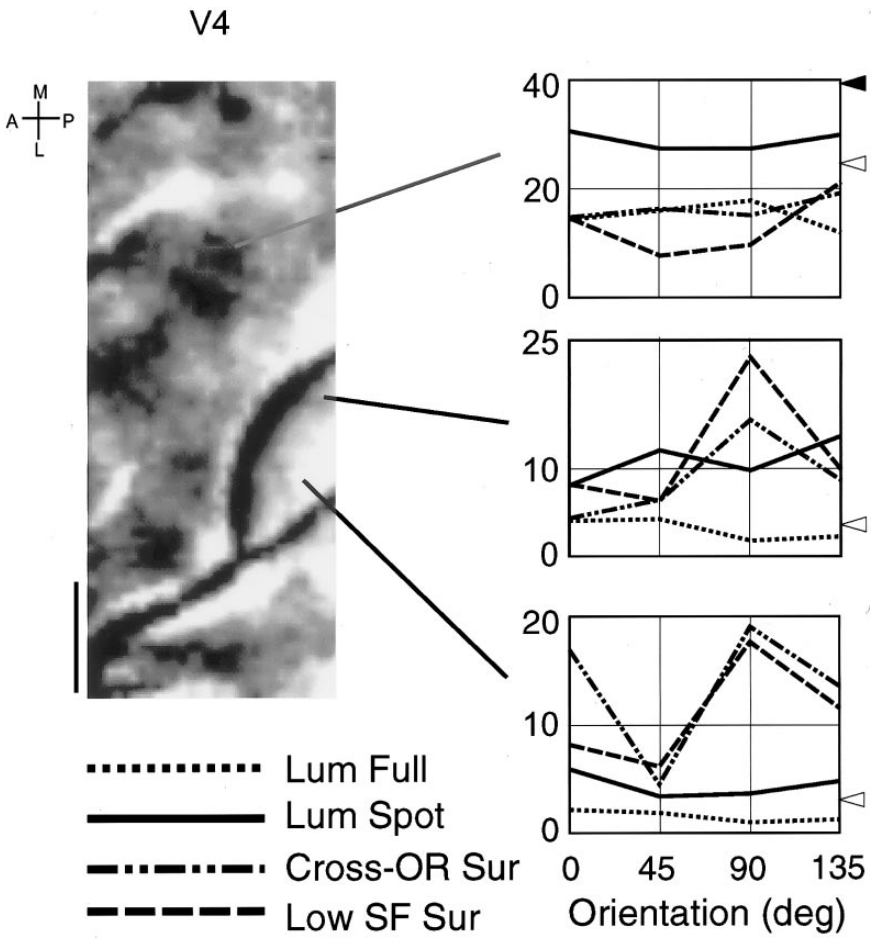

FIG. 2. Surround suppression is functionally organized within V4. Before imaging, electrode penetrations were made to localize the receptive fields of cells at a location in the center of the V4 exposure as well as cells located in the center of the V2 exposure. A pair of spots (V2: 1.25°; V4: 2.5°) containing square-wave gratings (1.8 cycles/degree) were positioned according to these receptive field locations. This pair was randomly interleaved with full-field gratings (22°). Dark regions of the image: preferential response to the smaller stimuli. Single cells at specific locations within the map were mapped to determine receptive field sizes and positions. Cells were then tested with a randomly interleaved stimulus set that combined sinusoidally modulated gratings at 4 different orientations within the receptive field (plotted along the *X*-axis) with a variety of stimuli surrounding the receptive field. Responses are plotted according to the average number of spikes observed during 2-s trials. Four types of surrounds were tested: mean luminance (Lum Spot), the same orientation and spatial frequency as the center (Lum Full), orthogonal orientation to the center (Cross-OR Sur), and 1/4 the spatial frequency of the center (Low SF Sur). Open triangles: spontaneous activity levels. Filled triangle for the cell within a subregion within V4 that preferentially responded to the smaller stimuli (S region; *top right*): response to the cell's optimal stimulus (chromatically modulated spot).

DISCUSSION

Imaging with small stimuli reveals two features of functional organization that appear to emerge in area V4: the distributed representation of small stimuli at the expense of precise retinotopy and the presence of S regions. The preferential response of large regions of V4 to small stimuli corroborates the hypothesis, suggested by lesion experiments (Schiller 1993), that size analysis is an important aspect of V4 visual processing. Although our data suggest that some S regions are specialized for color, we do not know whether submodules with different surround sensitivities exist within S regions. Given the spectral sensitivity of V4 surrounds (Desimone et al. 1985; Schein and Desimone 1990), chromatic S regions might play a significant role in perception of color constancy.

Functional organization in V4 has been suggested on the basis of three factors: *1*) the anatomic segregation of the inputs and outputs to the area (DeYoe et al. 1994), *2*) the presence of patchy long-range connections (Amir et al. 1993; Yoshioka et al. 1992), and *3*) limited electrophysiological recordings (DeYoe et al. 1992). Our results directly confirm the notion that functional segregation exists within V4 with respect to orientation, size, and color (Ghose and Ts'o 1995). These observations suggest that functional segregation is a general scheme of processing visual information among the different visual areas. However, functional organization in V4 is clearly distinct from that seen in the earlier visual areas. In areas V1 and V2, functional properties display a correspondence to the regular patterning of cytochrome oxidase activity (Hubel and Livingstone 1987; Malach et al. 1994; Ts'o et al. 1990). In area V4, however, there is no such pattern, and we found no obvious correspondence between the functional maps obtained through imaging and variations in cytochrome oxidase staining. In this regard, V4 appears similar to MT, in which functionally specific patterns seen with 2-deoxyglucose and optical imaging methods have little correspondence to cytochrome oxidase activity (Born and Tootell 1992; Malonek et al. 1994). The lack of correspondence between cytochrome oxidase staining and functional organization in both V4 and MT underscores the value of optical imaging in revealing patterns of segregation that are not accessible by common anatomic techniques.

The functional organization of V4 is distinctive in other regards as well. Large orientation-specific domains, for example, were only found in the foveal representation of V4. Thus functional organization within V4 seems to be highly dependent on eccentricity, a pattern that has not been reported in any other visual area. Although orientation tuning as a function of eccentricity has not been systematically studied in V4, we have found oriented cells outside the foveal representation, as have other investigators (Cheng et al. 1994; Desimone and Schein 1987; Desimone et al. 1985). We therefore think it unlikely that orientation information in V4 is strictly confined to the foveal representation. A more likely explanation is that

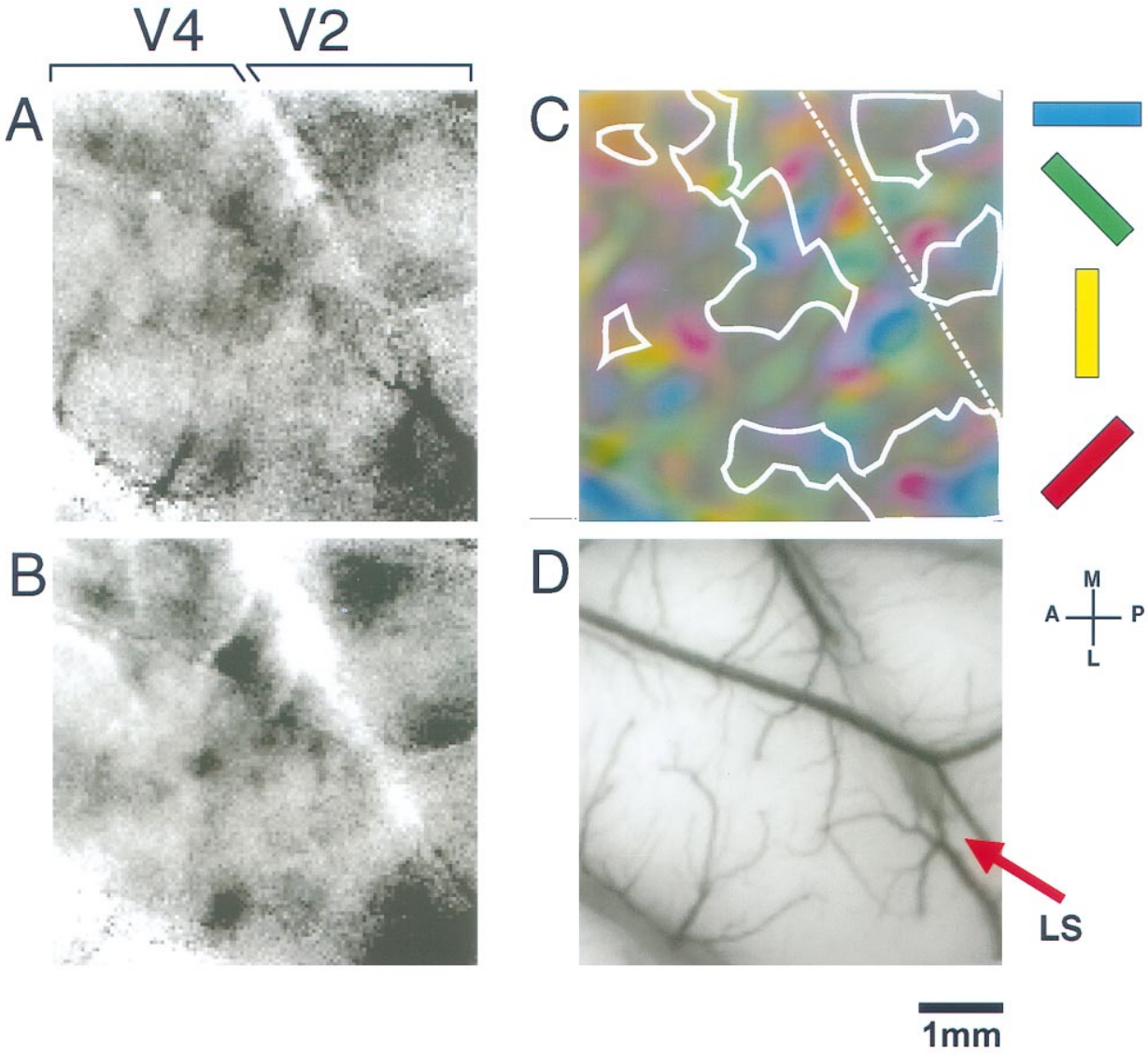

FIG. 3. Square-wave gratings (1.8 cycles/degree) of 4 different orientations and 2 different sizes (small: 1.25°; full field: 22°) were monocularly presented in a randomly interleaved manner. White diagonal line: lunate vessel, which defines the V4/V2 border within the images. An orientation map for the V4 portion is shown in Fig. 1*B*. *A*: imprecise retinotopy is demonstrated by subtracting images acquired when the cathode ray tube (CRT) was blank from images acquired during the presentation of the 1° stimuli (small − blank). Dark regions: responses to small luminance stimuli. Activation occurs across a considerably larger region of V4 than across V2. *B*: S regions are visualized by subtracting images acquired during full-field stimulation from images acquired with the small stimuli (small − full field). Dark regions indicate preferential responses to small luminance stimuli. In *C*, a contour plot of the S regions [defined by ($\Delta R/R > 3 \times 10^{-4}$)] is superimposed on a color-coded map of orientation preference. Color saturation within this map indicates orientation selectivity. Unlike in V2, S regions in V4 are not limited to unoriented regions, but can span isoorientation domains. *D*: lunate vessel is clearly visible in the vascular image. Note the lack of correspondence between this image and functional images in *A*–*C*.

parafoveally, oriented cells are not strictly organized into distinct domains that are visible by optical imaging. Imaging does reveal functional organization in parafoveal regions: we have observed, for example, color preference regions and S regions (Fig. 2) parafoveally as well as foveally (Ghose and Ts'o 1995). However, it is possible that parameters other than orientation are also differentially organized according to eccentricity. This possibility might explain why paired retrograde injections in inferotemporal cortex yielded segregated labeling in some regions of V4 and more continuous labeling in other regions of V4 (DeYoe et al. 1994).

Interestingly, functional organization with respect to surround interactions has also been found in owl monkey MT (Born and Tootell 1992). Thus both extrastriate areas contain assemblies of cells that could contribute to perceptual segregation and popout. According to this scheme, cells within the regions of MT analogous to S regions could provide information enabling motion-based segregation, whereas cells in the S regions of V4 could contribute to color- and form-based segregation and size analysis. Thus area V4, in the absence of obvious histological correlates, exhibits organizational principles seen in V1 (orientation

and color) as well as those seen in extrastriate area MT (surround suppression). These findings demonstrate that different areas within the cerebral cortex can share common strategies for organizing visual information into distinct functional streams.

We thank A. Roe for help with the experiments, as well as J. Maunsell, J. Assad, and C. Landisman for comments on the manuscript.

This work has been supported by grants from the National Eye Institute and the McKnight Foundation.

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Received 23 August 1996; accepted in final form 14 November 1996.

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