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Functional Anatomy of Macaque Striate Cortex. III. Color

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Using spatially diffuse stimuli (or sinusoidal gratings of very low spatial frequency), levels of ^{14}C-2-deoxy-*d*-glucose (DG) uptake produced by color-varying stimuli are much greater than those produced by luminance-varying stimuli in macaque striate cortex. Such a difference in DG results is consistent with previous psychophysical and electrophysiological results from man and monkey. In DG experiments with color-varying gratings of low and middle spatial frequencies, or with spatially diffuse color variations, DG uptake was highest in the cytochrome oxidase blobs, as was also seen with low-spatial-frequency luminance gratings. High-spatial-frequency, color-varying uptake patterns were shifted to cover both blob and interblob regions in a manner similar to that of the patterns obtained with middle-spatial-frequency luminance stimuli. However, in no instance did chromatic gratings produce uptake restricted to the interblob regions, as with the pattern seen with the highest-spatial-frequency luminance gratings. Thus, DG uptake is relatively higher in the interblob regions when comparing luminance with color-varying gratings that are otherwise similar. It was also possible to show DG evidence for receptive-field double-opponency in the upper-layer blobs, but color sensitivity in layer 4Cb appears single-opponent. The DG results suggest that color sensitivity is also high in the lower-layer (layers 5 + 6) blobs, and that many layer 5 receptive fields are double-opponent. Striate layers 4Ca and 4B appeared color-insensitive in a wide variety of DG tests; this supports the idea of a color-insensitive stream running from the magnocellular LGN layers through striate layers 4Ca and 4B to extrastriate areas MT and V3. There was also a major effect due to wavelength: long and short wavelengths produced much more uptake than did middle wavelengths, even when all colors were equated for luminance and saturation. No variation with eccentricity was seen in cortical color sensitivity, at least between 0° and 10°.

Although both chromatic and luminance variations are important carriers of visual information, many physiological studies of primate spatial vision have ignored color variations altogether. Presumably, this can be attributed to technical complications and to an attempt to simplify physiological testing procedures, which are already arduous. However, the macaque (like man) can perceive a whole gamut of color variations, in addition to variations in light intensity. The added dimension of color necessarily expands the machinery of vision and the attendant problems of understanding that machinery.

Both man and the macaque can discriminate about 100 variations of wavelength near the spectral locus (Wright, 1946; De Valois et al., 1974), and about 30–80 variations of spectral purity at each wavelength (MacAdams, 1942; De Valois et al., 1974), even when the stimuli to be discriminated are equated for luminance. Thus, several thousand color combinations can be discriminated at a given constant luminance level. A best estimate of the number of discriminable variations in intensity contrast (in a comparable spatial context for a single mean luminance) is only about 30 or less (Legge and Foley, 1980; Swift and Smith, 1983).

The number of discriminable colors rises to 7.5–10 million when variations in luminance, as well as color, are considered (Judd and Kelly, 1939; Nickerson and Newhall, 1943). From the latter estimates, the number of discriminable color–luminance *pairs* becomes $n(n-1)/2$, or about 5×10^{13}. Such a number is apparently formidable enough that computational models of spatial vision have simply ignored color borders altogether (see Marr, 1982), except in a few instances (e.g., Horn, 1974; Land, 1983). Unfortunately, the primate brain does not have the luxury of ignoring color variations in spatial vision: primate psychophysics and physiology indicate that spatial variations in color are actively extracted and used in a number of visual tasks (De Valois et al., 1974; Thorell et al., 1984).

In the natural world, spatial borders that differ in wavelength or saturation normally coincide with differences in intensity along the same object borders. Thus, in a highly retinotopic structure like striate cortex, color and intensity variations that are reflected from a single object discontinuity will perforce be processed in the same local striate region. Because of this retinotopic constraint, and because color processing adds a whole other dimension to striate image analysis, it may be presumed that a certain amount of striate architecture is devoted to organizing color and luminance information in parallel.

Early electrophysiological studies reported a relatively high percentage of color cells in some striate layers, and a low percentage in others (Dow and Gouras, 1973; Dow, 1974; Gouras, 1974). These studies suggest that there is a *laminar* organization of color. However, it has also been reported that striate color cells are grouped into columns running perpendicular to the laminae (Michael, 1981). An apparent synthesis of the 2 ideas

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has recently been furnished by Livingstone and Hubel (1984a, b), who report that large numbers of color cells are found in the upper-layer (and perhaps the lower-layer) cytochrome oxidase (cytox) blobs. Since the blobs are limited along both laminar and topographic axes, the "color in blob" notion can be thought of as both laminar and columnar. The "color in blob" idea is also supported by preliminary ^{14}C-2-deoxy-*d*-glucose (DG) evidence (Tootell and Silverman, 1981; Tootell et al., 1983a) and by an electrophysiological study using multiple electrode arrays (Kruger and Fischer, 1983).

It would be a mistake, however, to equate the architecture of the cytochrome oxidase blobs exclusively with color vision. The cytox blobs have been related to a wide variety of physiological and anatomical variables in the extragranular layers; color properties may be simply one of these variables. It should also be noted that other primate genera, such as *Aotus* and *Saimiri* (in which color vision is much restricted, or almost negligible, relative to that of the macaque), have cytochrome oxidase blobs in which the contrast and size of the stained blobs are about equal to that seen in the macaque. Even in comparisons of known protanopes to known trichromats of the same primate species, no difference in the contrast or architecture of the cytochrome oxidase blobs is evident (R. B. Tootell, M. S. Silverman, and J. H. Jacobs, unpublished observations). Finally, there are a number of other dark-staining cytochrome oxidase patterns in other visual and nonvisual cortical areas that are completely unrelated to color vision (Tootell et al., 1983a, 1985a).

Bearing these caveats in mind, the recent evidence for a color architecture that is related to the cytox blobs is nonetheless intriguing, and it raises a number of related questions. For instance, it would be interesting to find out how color is coded within the cytox blobs; perhaps some blobs are specialized for certain colors. Alternatively, there might be a subdivision of color specificity *within* each cytox blob.

It has also been reported that the receptive fields of many of the color cells in the upper layers are double-opponent in nature (Livingstone and Hubel, 1984a). Such a receptive-field arrangement is more complicated than that of color cells at more primary levels of the geniculostriate pathway (Livingstone and Hubel, 1984a; Michael, 1985). A "double-opponent" receptive field in the color domain eliminates the response to spatially diffuse color stimuli that is seen in single-opponent color responses at earlier levels (Livingstone and Hubel, 1984a; Thorell et al., 1984), yielding a bandpass spatial tuning for color stimuli instead of the low-pass spatial tuning seen in single-opponent receptive fields.

It would be interesting to know whether the receptive fields of cells in the lower-layer cytox blobs are also color-specific, and whether they are also double-opponent in nature. So far, however, the cells in the lower-layer blobs have been described only sketchily (Livingstone and Hubel, 1984a).

Finally, it would be interesting to trace the origins of the double-opponent cells in the cytox blobs. According to Michael (1985), double-opponent color cells in the upper-layer blobs may receive inputs from double-opponent cells in underlying layer 4Cb. However, according to other authors, all, or the overwhelming majority, of color cells in layer 4Cb have single-opponent receptive fields (Livingstone and Hubel, 1984a).

It would be very difficult (or, at best, extremely tedious) to answer all of these questions using electrophysiological techniques. Instead, we were able to gather evidence on these and related questions by using DG coupled with specific visual stimulation and extensive control manipulations. The DG approach also allowed us to address other, more general questions about color architecture that are not related to the blobs.

For instance, we wondered whether it would be possible to trace the segregation of color information all the way through striate cortex, or only into striate layers receiving and sending projections to other areas. Parvocellular cells are in general more sensitive to variations in color than are magnocellular cells (De Valois et al., 1966; Wiesel and Hubel, 1966; Schiller and Malpeli, 1978; Derrington et al., 1984). Since the major projections from magno- and parvocellular layers terminate in strictly segregated layers within striate cortex (4Ca and 4Cb, respectively) (Hubel and Wiesel, 1972; Hendrickson et al., 1978), it is logical to assume that these striate layers would also differ in their sensitivity to color-varying stimulus patterns. In the present study we have examined this question, and have attempted to trace this color segregation through subsequent striate layers.

There is also evidence for a segregation of luminance and color signals in the striate projection to second-tier cortical visual areas. For example, layer 4B of striate cortex sends a major projection to cortical area MT (Lund et al., 1976), and it has been reported that there are no color cells in MT at all (see Zeki, 1978). In contrast, other layers of striate cortex (2 + 3) project to cortical area V2, which contains a high percentage of color cells (Burkhalter and Van Essen, 1982). Presumably, then, one might expect some anatomical segregation of color and luminance signals in striate cortex, if only to send the correct kinds of information to the correct extrastriate regions. In this study, we present DG evidence that striate layers that project to MT and V2 have color and luminance sensitivities that match those of the corresponding projection areas.

We have emphasized the segregation of color and luminance in the LGN and striate cortex, but in fact many cells in these areas respond to both color *and* luminance (De Valois et al., 1977; Gouras and Kruger, 1979; Hicks et al., 1983; Derrington et al., 1984; Thorell et al., 1984). In both areas, there is some evidence that receptive-field sensitivity profiles for color and luminance are different in a significant population of cells. The generality that emerges from both electrophysiological (De Valois et al., 1977; Hicks et al., 1983; Thorell et al., 1984; see also Kruger and Gouras, 1980) and psychophysical (Van der Horst and Bouman, 1969; Granger and Heurtley, 1973; Watanabe et al., 1976) evidence is that color sensitivity remains relatively high even at very low spatial frequencies, although luminance sensitivity is markedly decreased at these frequencies. At high spatial frequencies, the reverse is true (perhaps because chromatic aberration makes chromatic sensitivity at high spatial frequencies irrelevant). By manipulating the spatial frequency of color-varying and luminance-varying stimulus patterns in DG studies, we examined the functional evidence for such a spatiochromatic interaction, and tried to gain some insight into the architectural strata underlying it.

We also describe a series of experiments aimed at clarifying the organization of color relative to the cytochrome oxidase blobs—that is, determining whether different colors, or hues, are coded in different blobs (e.g., Dow and Vautin, 1986) or in different portions within each blob. In the course of this analysis of hue architecture, it became evident that different stimulus wavelengths produce vastly different levels of DG uptake, even when the different wavelengths are equated for luminance and spectral purity. Because the nature of this wavelength bias resembles the Old World primate saturation function, we per-

formed a psychoanatomical experiment designed to quantitatively relate the primate saturation function to the DG wavelength bias.

Materials and Methods

Surgical and histological procedures used in this study are identical to those described in the first paper in this series (Tootell et al., 1988a). Briefly, macaques were anesthetized, paralyzed, and prepared as if for single-unit recording (which was sometimes done in conjunction with the DG experiments). The eye(s) was focused and optically arranged so that the foveal projection of each eye (or, in monocular experiments, the open eye) was centered on the stimulus screen. DG was injected while the monkeys viewed the chosen stimulus; individual stimulus parameters are described more fully below. Monkeys were then euthanized and transcardially perfused with a phosphate-buffered formalin solution, and the brains removed. In the first 5 monkeys, the brains were frozen and cut in a cryostat in the conventional manner. In subsequent monkeys, the opercular striate cortex was dissected free and frozen while in a flattened state, and then sectioned in a cryostat. Sections from the flattened brains were almost always cut parallel to the surface of the flattened cortex. Subsequent autoradiographic processing was standard, with modifications to permit cytochrome oxidase histochemistry (M. S. Silverman and R. B. H. Tootell, unpublished observations).

One major experimental comparison made was between the effects of color-varying and luminance-varying stimuli on patterns of DG uptake. Thirty-five macaques were shown black–white patterns, and 9 macaques were shown color-varying stimuli (for specific stimulus conditions, see Table 1 in Tootell et al., 1988a). Another 11 macaques (not included in the above samples) were shown visual stimuli in which the visual field was divided into 2 or more regions: one region contained a color-varying stimulus, and the other contained achromatic variations in luminance (split-field tests; cases 23, 25, 27, 29, 33, 34, 36, 38, 41, 48, 53). Many of the animals shown black–white stimuli were also used in other experiments. Both color- and luminance-varying stimuli were generated on a Tektronix 690 monitor. C.I.E. coordinates for the colors normally used in these experiments were as follows: red, 0.627, 0.326; green, 0.318, 0.586; blue, 0.134, 0.055; yellow, 0.475, 0.457; purple, 0.395, 0.199; and white, 0.309, 0.314. In some experiments, the spectral purity of the colors was decreased by mixing in known amounts of white.

The intensity of all hues was adjusted so as to be equal in luminance according to the C.I.E. photopic luminance curve, and was thus approximately equated in luminance for each macaque (De Valois et al., 1974). Luminance was calibrated using a Pritchard photometer. Stimulus mean luminance was set at 34–86 cd/m^2. Experiments were run below 86 cd/m^2 only when limited by the light output of individual phosphors. A white mask surrounded the stimulus screen and photopic conditions were maintained across the retina by keeping the room lights on.

The Michelson contrast of the luminance-varying patterns was set at 100%, which was effectively closer to 95% with the room lights on. The color-varying patterns corresponded to modulation (either sinusoidal or as a square wave) between pure phosphor loci or between phosphor loci and white, except when corrections were made for spectral purity. For example, a red–green grating was produced by summing a red–black grating with a green–black grating of equal contrast, 180° out of phase. Spatial aspects of the individual stimuli are described case by case below.

Results

Spatially diffuse stimuli

General results

It has been demonstrated that many LGN cells will respond to both color and luminance variations, but that the spatial sensitivities in the color and luminance domains are quite different within a given cell (De Valois and De Valois, 1975). The center–surround antagonisms of different cone inputs in the classical single-opponent geniculate cells lead to a marked decrement of responses to very spatially diffuse (or very low spatial frequency), luminance-varying stimuli. However, the response of such "single-opponent" cells to spatially diffuse, color-varying stimuli is not decreased because the different cone inputs in such a situation actually synergize (De Valois and De Valois, 1975). (Thus, in some sense, the term "single-opponent" is a misnomer; we use the term because it has wide currency.)

Because the difference in geniculate response to color- and luminance-varying patterns is greatest in response to spatially diffuse (very-low-frequency) stimuli, we used spatially-diffuse stimuli in our initial studies of the striate color architecture (Tootell et al., 1980; Tootell and Silverman, 1981) in an attempt to isolate the color architecture more completely. Because there were no spatial variations in these early stimuli, problems of interpretation that might be due to binocular disparity cues, chromatic aberration, optical quality, or other spatial contingencies did not arise. Because the interpretation of results from these cases can be divorced from spatial variables, the spatially diffuse results serve as useful reference conditions for cases described later, using spatially patterned color and luminance stimuli.

In the diffuse-stimulus experiments we simply moved the monitor screen close to the animal, opened and defocused both eyes by several diopters (to blur out individual pixels), and programmed the entire display screen to change in either color or luminance in a temporal square wave at 0.5–4 Hz. Four monkeys were shown diffuse-field stimuli that varied temporally between a given single color and an equiluminant gray, and, in one monkey, between one color and another (cases 1, 3, 5, 6). Two other monkeys were shown diffuse field stimuli that flickered between a very dark gray and white (luminances of about 3.4 and 103.8 cd/m^2, respectively; cases 2, 7).

The results from these first color-varying cases are shown in Figures 1 and 2, which include representative autoradiographic sections from 2 animals, each of which binocularly viewed a spatially diffuse red–gray stimulus. Results from both animals were quite similar. In conventional sections cut oblique to the cortical surface (Fig. 1), as well as in flattened sections (Fig. 2), a characteristic spotty pattern of DG uptake can be seen throughout layers 1–3, and again in layers 5 and 6. DG uptake in layer 4B is only marginally above unstimulated levels, and it is topographically uniform. In layers 4A and 4C, the pattern is dark and continuous.

One of the most significant of the laminar differences in these full-field, color-varying cases occurs between the 2 layer 4C subdivisions. Quantitatively, levels of uptake in 4Cb are 5–10 times higher than those in 4Ca, after the baseline uptake in unstimulated regions of the same layers is subtracted out (see below). The increased uptake in layer 4Cb in response to full-field color stimuli agrees very nicely with electrophysiological differences in the color sensitivity and receptive-field properties of cell bodies and afferent terminals in layers 4Cb and 4Ca (Blasdel and Lund, 1983; Blasdel and Fitzpatrick, 1984; Livingstone and Hubel, 1984a). From the data of Livingstone and Hubel (1984a, b), one would expect cells in layer 4Cb to respond in a manner similar to that seen in single-opponent color cells (which respond optimally to full-field color changes), and one would expect cells in layer 4Ca to respond poorly to full-field color changes. The low uptake in layer 4B is cognate with the minimal activation of layer 4Ca, from which 4B derives much of its input (Lund and Boothe, 1975; Blasdel et al., 1985; Fitzpatrick et al., 1985; Tootell et al., 1988b).

The spotty pattern of DG uptake in the extragranular layers, in fact, lies in the cytochrome oxidase blobs (demonstrated below). The point we wish to make here is that the levels of uptake in both the *upper*- and *lower*-layer cytox blobs are quite high in

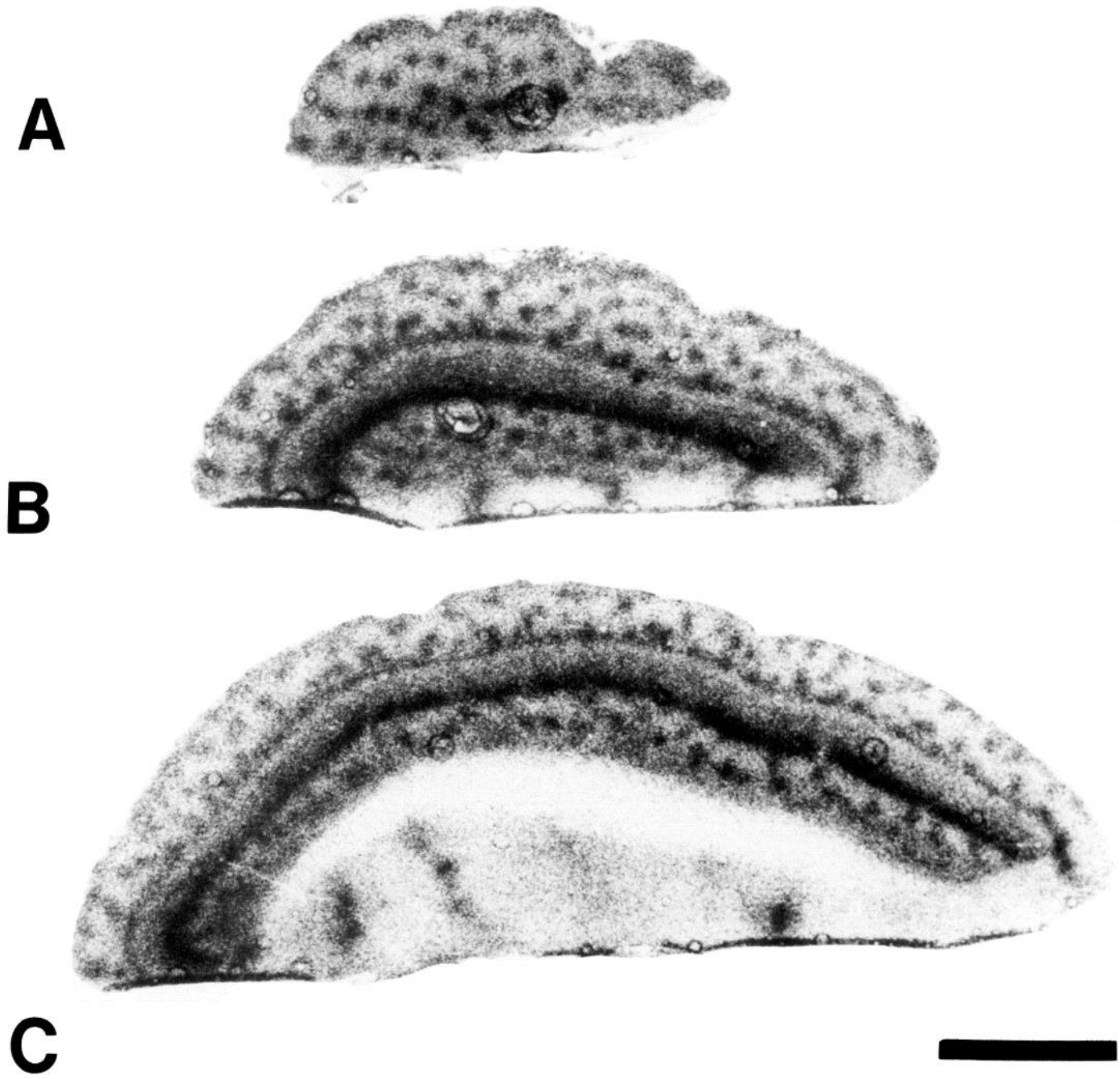

Figure 1. DG autoradiographs from an animal that viewed a spatially diffuse screen, flickering between red and an equiluminant gray at 3 Hz. Viewed binocularly. *A–C* Taken from 3 sections, cut oblique to the surface from an unflattened tissue block at successively deeper levels. The bottom of the section in *C* (and the very bottom of the section in *B*) passes through V2; the more intricate DG pattern in the top portion of *A–C* is striate cortex. *A*, The pattern of DG uptake in layer 3, grazing layer 4A. In *B* and *C*, one can see (from top to bottom) the blob uptake in layers 2 + 3, a thin strip of high uptake in 4A, low uptake in 4B, slightly higher uptake in 4Ca, high uptake in 4Cb, and high uptake in the cytox blobs in layers 5 + 6. The pattern of DG uptake is very similar to the architecture of the cytochrome oxidase stain itself, except in 2 respects. First, layers 4Ca and 4Cb stain equally dark following cytox staining, but in this case they take up quite different levels of DG. Second, the lower-layer blobs stain only faintly with the cytox stain, but are robustly labeled with DG here. Scale bar, 2.5 mm.

these DG results, whereas, in the macaque, only the *upper*-layer blobs are clearly visible when stained for cytochrome oxidase (see Horton, 1984; Livingstone and Hubel, 1984a; and ocular dominance section). This strongly suggests that the functional segregation of bloblike properties in the upper striate layers is reflected in the lower layers, though this segregation is not as visible with the cytochrome oxidase stain itself. Interblob areas in layer 6 take up more DG than do corresponding areas of layer 5. Since the level of DG uptake in the lower-layer cytox blobs is about the same in both layers, the contrast between the cytox blobs and the non-blob areas is thus greatest in layer 5 (see Fig. 2).

To examine the functional anatomy of spatially diffuse variations in *luminance,* we showed 2 monkeys full-field stimuli

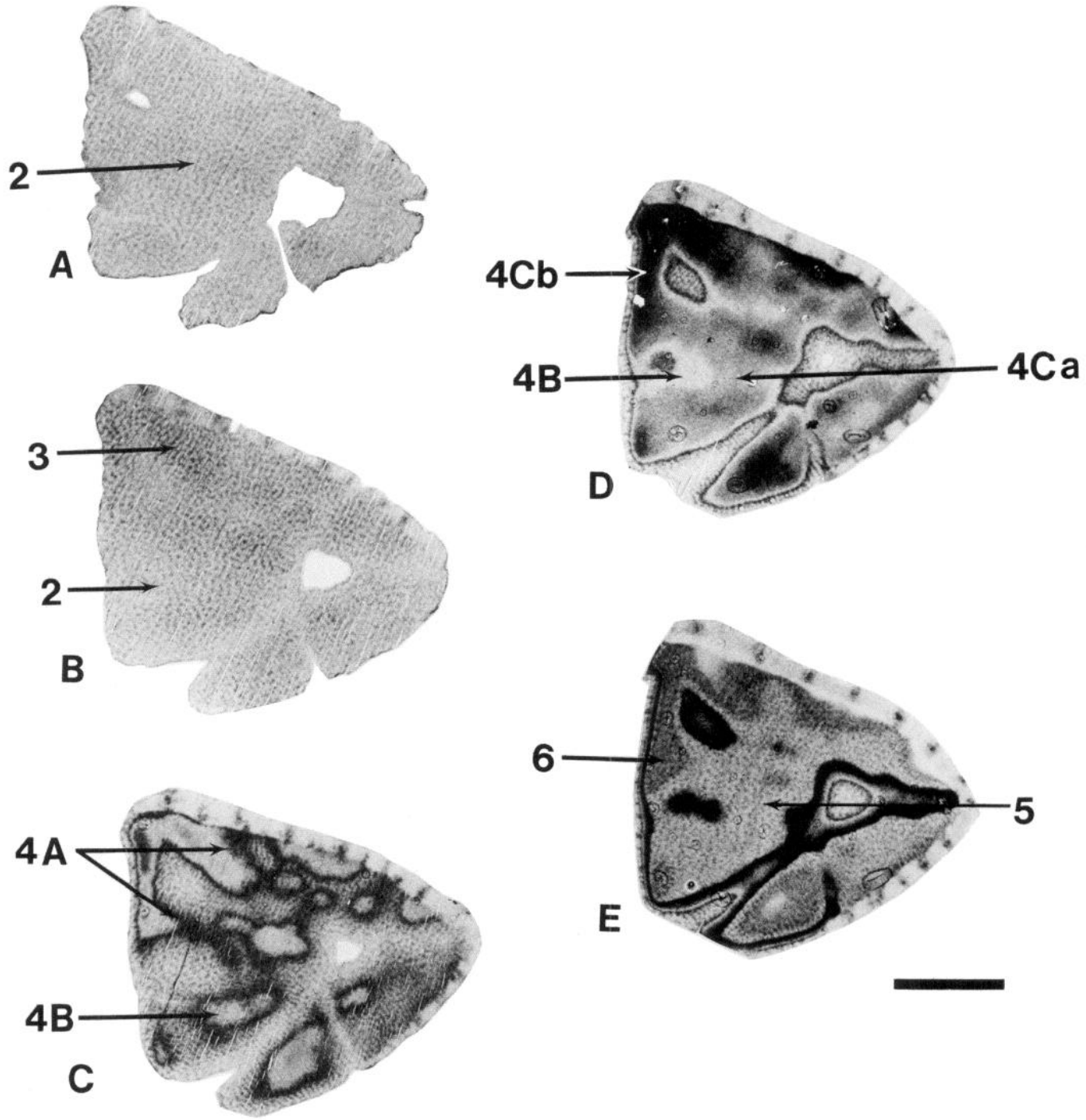

Figure 2. DG autoradiographs from another animal, visually stimulated as in the case in Figure 1, but sectioned from a flattened block. Many of the laminar variations visible in Figure 1 can be seen in the 5 successively deeper sections. For instance, levels of DG uptake are approximately equivalent in the upper- and lower-layer blobs (compare *B* and *E*), and uptake in parvorecipient layer 4Cb is much greater than that in magnorecipient layer 4Ca (*D*). In addition, one can see that uptake in the interblob areas of layer 6 is higher than that in the interblob areas of layer 5, and that uptake in layer 2 is less than that in layer 3. The latter laminar difference is quite common to other stimulus–DG combinations. Scale bar, 1 cm.

that changed from black to white at a rate equal to that used in the diffuse-field color experiments (cases 2, 7). The result was quite straightforward: diffuse luminance changes of a log unit or more produce very little or no DG uptake at all in striate cortex (see Fig. 3). The autoradiographs from these cases look very much like those from animals viewing a diffuse gray screen (see Tootell et al., 1988a). Levels of uptake in the cytox blobs and in all layers are approximately equal to those outside the visually stimulated area. In fact, the difference in DG uptake between stimulated and unstimulated areas was so negligible that in one of these cases the border between stimulated and unstimulated regions was impossible to see.

To be certain that these spatially diffuse color–luminance differences were not simply due to variability between animals,

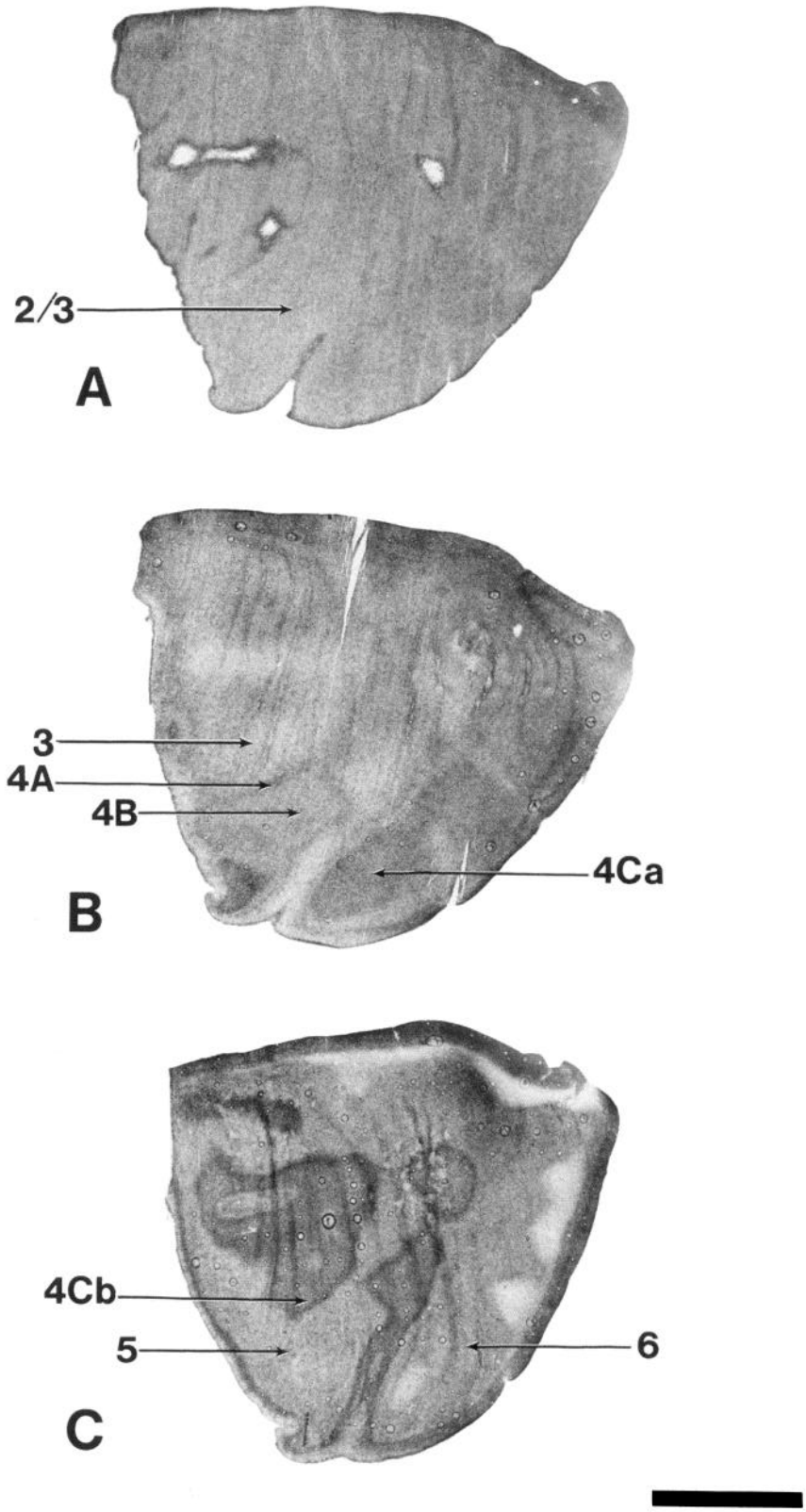

Figure 3. DG autoradiographs produced by spatially diffuse variations in luminance. The monkey in this case viewed a spatially diffuse stimulus identical to that described in Figures 1 and 2, except that it varied between black and white (103.8 vs 3.4 cd/m^2, respectively), instead of between red and gray. In the absence of discrete spatial borders, this large temporal variation in luminance caused very little stimulus-related uptake in any layer. This stimulus causes a very slight increase in DG uptake in the upper- and lower-layer blobs and 4Ca, which is consonant with (but a reduced version of) results from stimulation with an achromatic, low-spatial-frequency grating at all orientations. However, this subtle increase in DG uptake is nothing like that seen following stimulation with red–gray stimuli (see Figs. 1 and 2). The various layers are indicated with *arrows*. Calibration bar, 1 cm.

we tested the differences using a split-field stimulus pattern. In this case, one stimulus region contained spatially diffuse red–gray flicker, and an adjacent region contained spatially diffuse black–white flicker. In this case, the spatially diffuse variations took the form of a very low (0.1 cycle/deg) sinusoidal spatial frequency grating presented at all orientations and at a temporal frequency of 3 Hz (that is, a relatively fast velocity of 30 deg/sec). In a localized striate region, this stimulus was thus essentially equivalent to a spatially diffuse, sinusoidal temporal modulation along either the red–gray or black–white axis.

We showed this stimulus to a monkey through one eye (case 48). As can be seen in Figure 4, the red–gray segment is very effective in producing DG uptake, while the black–white segment is not. Because the stimulation was monocular, only half of the cytochrome oxidase blobs are activated in the red–gray section.

A sinusoidal temporal modulation of spatially diffuse stimuli (varying either in color or luminance) is conceptually equivalent to a drifting sinusoidal grating of extremely low spatial frequency. In the split-field experiment described above, results produced by sinusoidal color- or luminance-varying gratings of very low spatial frequency were indistinguishable from those produced by full-screen variations in either color or luminance, except for differences related to the monocular versus binocular exposure conditions. These robust differences in the DG effects of color and luminance stimuli at very low spatial frequencies support the idea that the color system as a whole has little low-spatial-frequency attenuation, whereas the luminance system as a whole is strongly attenuated at low spatial frequencies (Van der Horst and Bouman, 1969; Granger and Heurtley, 1973; Watanabe et al., 1976). On a more ancedotal level, the lack of DG uptake in response to diffuse-field luminance changes confirms the common observation that striate cells do not respond to changes in diffuse achromatic illumination when room lights are turned on or off during an experiment. The shift in DG effect with spatial frequency (both for color and luminance) is discussed in greater detail below.

Because large variations in the luminance of spatially diffuse stimuli had such a negligible effect on striate DG patterns, we feel confident that the elaborate DG patterns produced by nominally "equiluminant" variations in color are not confounded by possible minor errors in equiluminance calculations, at least when spatially diffuse stimuli are used.

Hue tests

The absence of significant DG uptake in the diffuse achromatic cases allowed us to isolate and label the metabolic activity produced by different hues simply by flickering a given hue against gray. For instance, the pattern of DG uptake in Figures 1 and 2 can be attributed to the red component of the red–gray color change, because spatially diffuse shifts in luminance (light-to-dark gray flicker) produced very little or no uptake. To examine the patterns of uptake produced by shifts to hues other than red, we placed a variety of single hues against gray, using different hues in different animals. In these tests it appeared that the *pattern* of DG uptake produced by different hues was identical (described below), but the *levels* of uptake that these hues produced differed markedly. However, a difference in DG contrast could also be due to uncontrolled variability between animals, so a more definitive test was necessary.

We therefore programmed a split-field stimulus in which the stimulus screen was divided into pie-shaped wedges of single, equiluminant hues, all of which were modulated against a solid, equiluminant gray (see Fig. 5). In all, 3 such experiments were done with spatially diffuse stimuli (cases 23, 33, 41). In these experiments, the eyes were not defocused. In the first experiment, we divided the screen into 8 wedges (2 mirror-symmetric sets of 4 colored wedges per hemisphere), and counterphased the pattern against an equiluminant gray at 1–4 Hz. One eye was occluded and the foveal projection of the other eye was centered on the middle of the pie-shaped stimulus.

Six representative sections from one hemisphere of this case

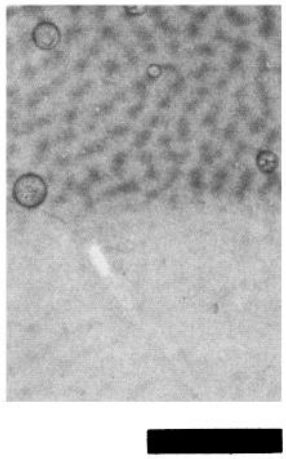

Figure 4. Split-field comparison of effects of diffuse variations in color (*top*) versus diffuse variations in luminance (*bottom*) in a section taken entirely from layer 3. The border between the color- and luminance-varying regions lies along the horizontal meridian, near the middle of the figure. The stimulus was viewed monocularly, so that only half of the cytochrome oxidase blobs in the color-stimulated region are labeled. Though the luminance-varying portion of the stimulus produces some very light stimulus-related uptake, uptake in the color-varying region is much higher. Scale bar, 5 mm.

are shown in Figure 5. For all hues, the pattern of the DG uptake is a monocular version of that shown earlier in Figures 1 and 2: half the cytox blobs are labeled with DG in the upper and lower layers, and dark ocular dominance strips are present in layer 4Cb, but only very lightly in 4Ca and 4B. However, a clear difference in the *effectiveness* of different hues in producing DG uptake is also apparent. For this particular set of stimulus hues, DG uptake produced by red is slightly greater than that produced by blue, which, in turn, is greater than that produced by green or yellow (the green–yellow effects are indistinguishable in Fig. 5).

One possible explanation is that the differential effectiveness of the different stimulus hues might be caused by confounding differences in the spectral purity of the stimuli. That is, the DG effect might conceivably have been produced by uncontrolled differences in the purity of the 3 colored stimulus sectors. In fact, a rank-ordering of the spectral purity of the different stimulus hues used in the experiment (blue = 0.98; red = 0.91; green = 0.86; yellow = 0.85) is somewhat similar to the order of the resultant DG effects. Thus, the shift in purity (from gray to a given hue) was larger for the blue and red than for the green–yellow, and the DG uptake was also larger for blue and red than for the other 2. However, in this animal there is a clear reversal in the DG effect relative to the respective purities of red and blue. Furthermore, it seems unlikely that such minor differences in spectral purity could have such a major effect on DG uptake.

These differences in stimulus purity nevertheless suggested a control experiment. The stimulus in the control experiment was similar to that described above, except that this stimulus had 6 sectors instead of 8 (thus, 3 hues per hemisphere), and the different hues were equated for purity as well as for luminance. In order to accomplish this, known amounts of white were substituted for red and blue in each of those sectors, so that the red and blue sectors had the same purity as the green. Since green had the lowest purity of the 3, it was of course not mixed with white. Yellow was not used in this test. Again, the experiment

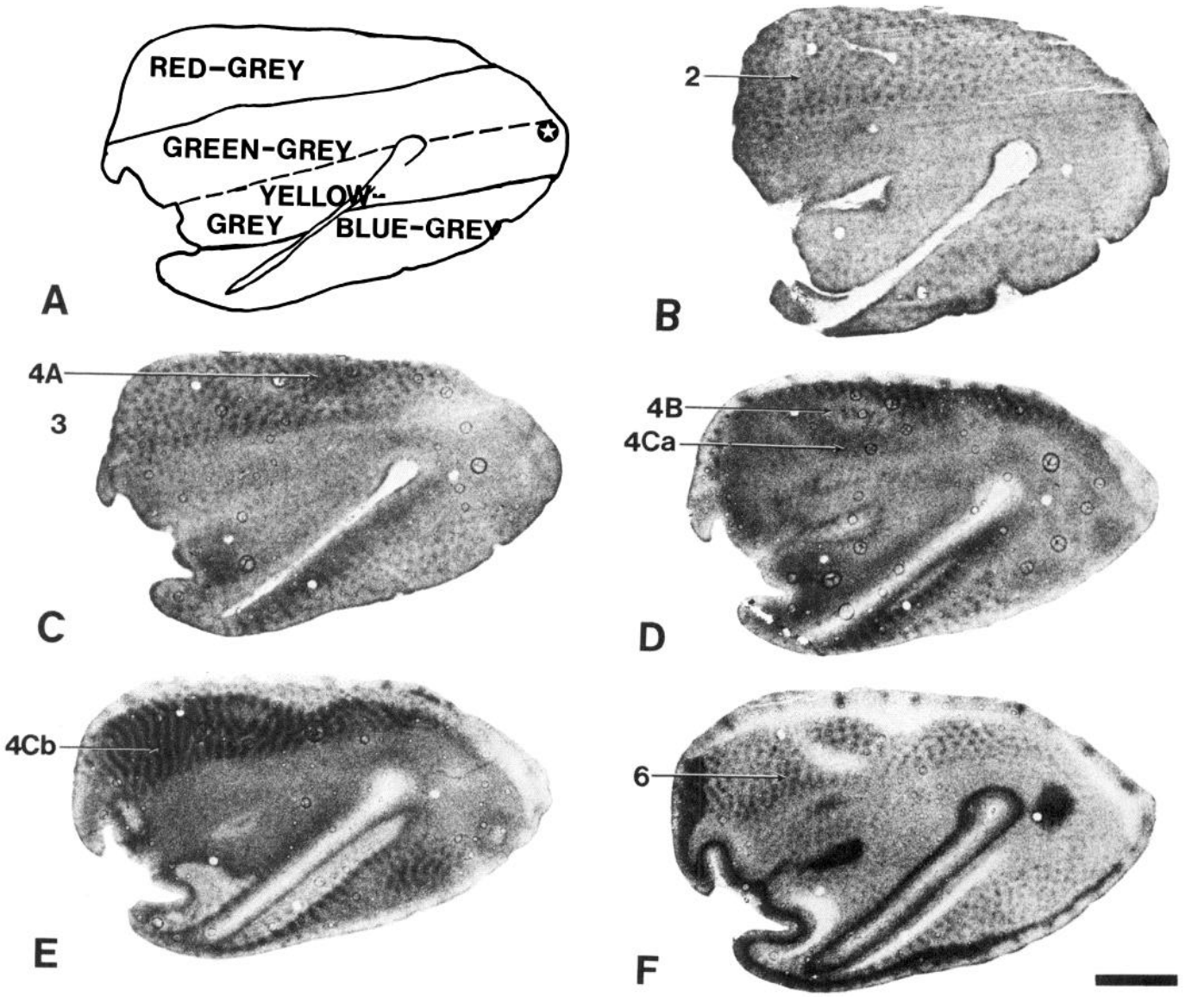

Figure 5. Split-field DG comparison of the effects of different wavelengths, each flickering against an equiluminant gray (which causes no uptake itself; see Figs. 3 and 4). Except for the borders between the different hue sectors, the stimulus was spatially diffuse. *A*, Diagram of the limits of the different stimulus hue sectors as they appear on the hemisphere illustrated in *B–F*. *B–F*, Successively deeper sections from a single flattened operculum. *B* cuts mostly through layer 2, *C* through layers 3 and 4A, *D* through 4B and 4Ca, *E* through 4Cb, and *F* through layers 5 and 6. A red–gray wedge projected to the top portion of *B–F*, a green–gray wedge to the upper center, yellow–gray to the lower center, and a blue–gray wedge projected to the bottom portion. Representative patterns of uptake are indicated for each layer within the red–gray sector at the ends of the *arrows*. Uptake produced by the red is slightly greater than that produced by the blue, and is clearly superior to that by the green and yellow wedges (which are indistinguishable owing to the relative lack of stimulus-driven uptake). These differences can be seen in every layer except in layers 4Ca and 4B (*D*): in the magnocellular-driven layers, the spatially diffuse color variations produce very little color-driven uptake irrespective of wavelength. Scale bar, 5 mm.

was done monocularly and the open eye was adjusted so as to view the center of the stimulus pattern.

The results of this manipulation are shown in Figure 6. It can be seen that even when the purity is equated, there is a marked decrease in the effectiveness of the middle wavelengths in causing DG uptake. The minor correction for spectral purity seems to make correspondingly little difference.

The nature of the wavelength bias in the DG effect suggested a relationship to the Old World primate saturation function. Saturation is the psychophysical analog of physical purity: wavelengths at which there is a high sensitivity to variations in spectral purity are said to be highly saturated. It has long been known (Purdy, 1931) that different spectral regions are not equally saturated. In the macaque and the human, the long- and short-wavelength regions of the spectrum (the reds and blues) are highly saturated, and the least saturated region is near 540 nm, a greenish–yellow (De Valois et al., 1974). So although the hues used in the previous case were equated for purity, the red and blue sectors were considerably more saturated than the green, and these sectors also produced more DG uptake.

We reasoned that if DG uptake was in fact coupled to saturation, then hues that had been equated for saturation should

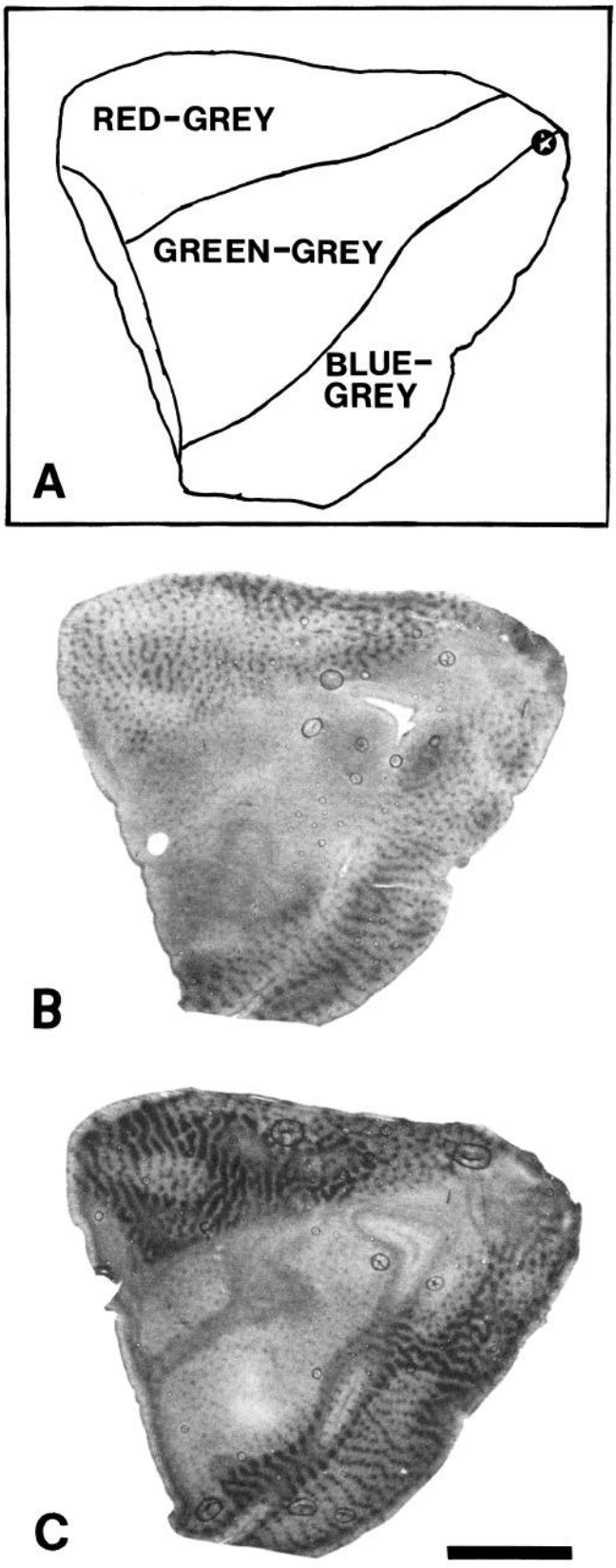

Figure 6. Split-field DG comparison of the effects of 3 different wavelengths (spatially diffuse and counterphased against a gray) when the wavelengths have been equated for spectral purity. The sections used were cut from a flattened operculum in an animal that had been monocularly exposed to (from *top to bottom*) red–gray, green–gray, and blue–gray. The retinotopic representation of the different hue sectors on the cortex appears in *A*. *B* is taken mostly from layer 3, grazing through 4A, and dipping into 4B in a few places. *C* cuts through layers 4Cb (dark ocular dominance strips) and layer 5 and 6 (strings of blobs). Again, wavelengths at the spectral extremes (e.g., red and blue) are clearly superior to middle wavelengths (such as green) in producing DG uptake. Scale bar, 1 cm.

produce equal DG uptake in striate cortex. In order to test this notion, the hues in each sector were equated for saturation by setting the saturation of each color at the same number of just-noticeable saturation steps from white. This was done by having the experimenter record the number and purity of just-noticeable differences (JNDs) in saturation from our white value to each of the red, blue, and green phosphor loci, all within an equiluminant plane. Saturation JNDs were measured on the same color monitor as was used in the DG experiment, and under the same lighting conditions.

Using the method of adjustment and 2 runs for each phosphor, we counted 60 and 66 JND steps for the red, 46 and 47 for the blue, and 36 and 32 steps for the green. Equal-saturation values for the red and blue were taken to be the purity at 34 steps from white (the mean number of saturation JNDs obtained for the green). The equal-saturation red obtained from these measurements was actually 62% white, and the equal-saturation blue, 35% white. The green (and most desaturated) phosphor was of course unmixed with white.

These equal-saturation values were presented to a monkey in the form of a circular-sectored stimulus much like those described earlier. One hemisphere was shown 3 equal-saturation sectors, and for a control the other was shown the 3 equal-purity sectors shown in Figure 6. The results are displayed quantitatively in Figure 7. It can be seen that the equal-saturation red and blue are still slightly more effective than the green in producing DG uptake, even at these drastically reduced purities. Therefore, either the difference in DG uptake is unrelated to saturation, or our test of the link was faulty in some way.

There is another important question that we can answer by closely examining the patterns of DG uptake in response to different hues. It has been suggested that striate cells that are specific for certain hues are grouped together in hue columns (Michael, 1981), but this initial report has never been confirmed. If such an anatomical segregation exists, it might take the form of a systematic relationship between periodicities in the DG labeling pattern and the pattern of cytochrome oxidase blobs. On the other hand, there is one preliminary report that maximum DG uptake occurs *in* the cytochrome oxidase blobs, apparently irrespective of hue (Tootell and Silverman, 1981). Both possibilities can be examined simply by comparing the position of the cytochrome oxidase blobs to the spotty regions of high DG uptake in response to different hues.

In this experiment we examined the cytochrome oxidase and DG patterns in the same sections from the monkey shown in Figure 7. The topography of DG uptake produced by red is shown in Figure 8*A*, that produced by blue in Figure 8*B*, and that produced by the green is not illustrated. For all hues, each spotty region of high DG uptake coincides with a cytochrome oxidase blob. A priori, one might have assumed that some sort of labeled line mechanism for different hues must have been preserved through striate, and that this might result in hue columns mapped in a systematic way relative to the cytochrome

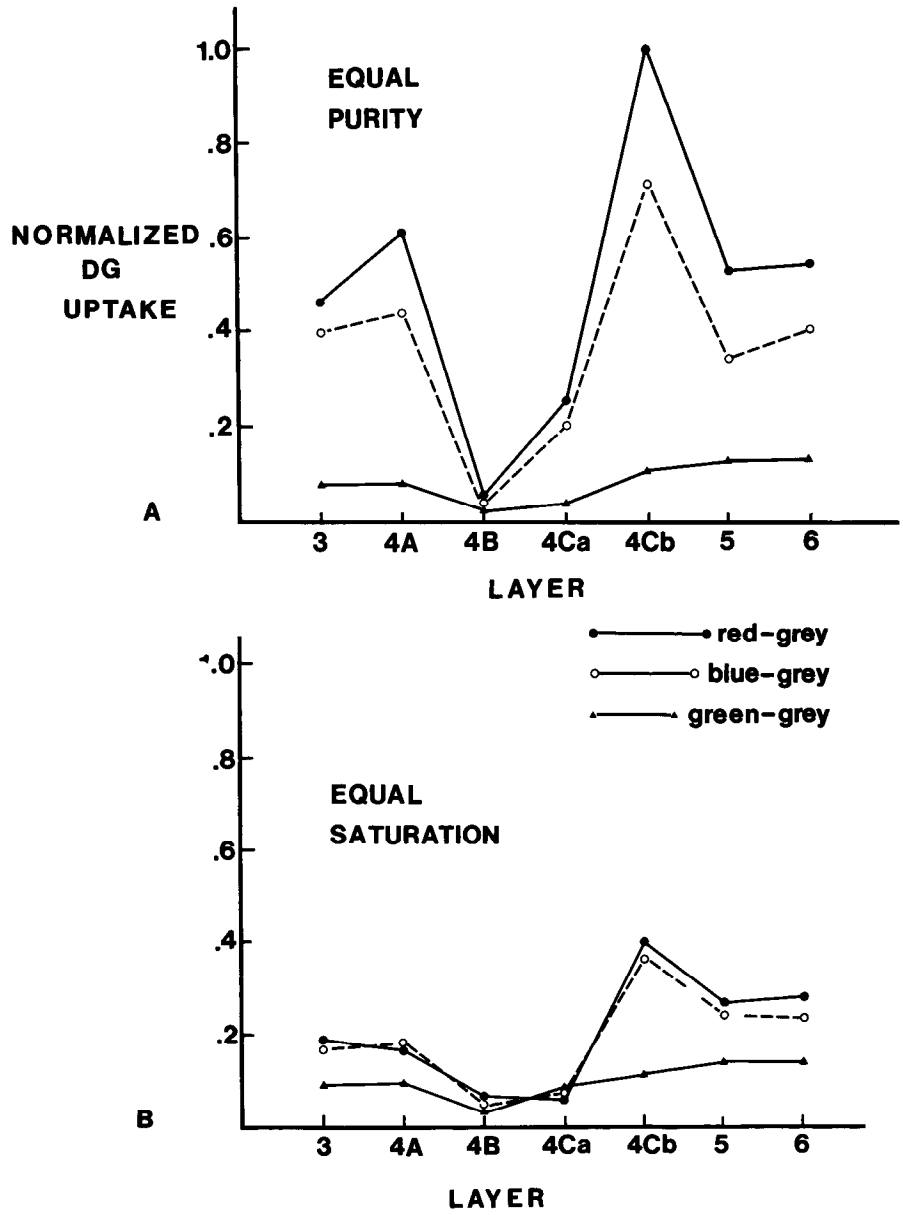

Figure 7. Densitometric analysis of an animal shown an equal-purity stimulus in one hemisphere, as described in Figure 6 (*A*), and an equal-saturation stimulus in the other hemisphere (*B*). In each hemisphere, the stimulus was divided into 3 sectors (each a different spatially diffuse color) and this stimulus was flickered against an equiluminant, spatially diffuse gray. In each hemisphere, the density of uptake produced by either the red, the blue, or the green stimulus was measured by averaging 30–50 samples from stimulated minus unstimulated portions of each layer, for different layers. Optical densities were converted to levels of deoxyglucose uptake by using radioactive standards. Uptake produced by the red is indicated by *filled circles,* by the blue by *unfilled circles,* and by the green by *filled triangles.* Uptake produced by the green–gray stimulus was averaged across both hemispheres, since the stimulus was identical on both hemispheres. The red–gray and the blue–gray stimuli were reduced in purity by 62 and 35%, respectively, in the equal-saturation stimulus (*B*). However, the red and blue segments still produced higher levels of uptake than the green–gray of much higher spectral purity.

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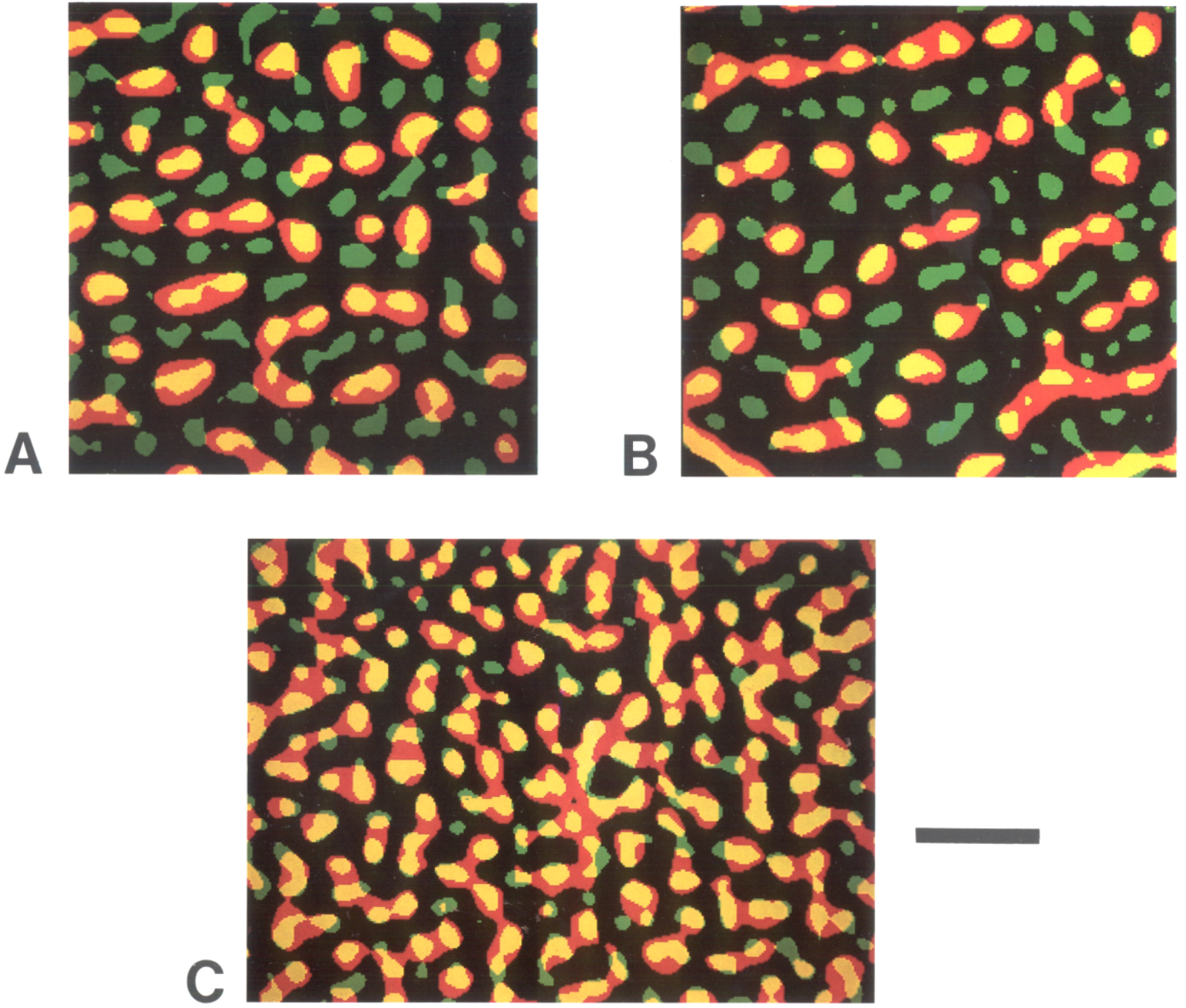
Figure 8. Densitometric analysis of the topographic relationship between cytochrome oxidase activity and DG uptake, in response to various visual stimuli. In *A–C,* measurements are made within a single section taken from layer 3 of macaque striate cortex. Regions of cytochrome oxidase activity above a certain densitometric level are color-coded *green,* and regions of high DG uptake are color-coded *red.* Regions of low DG uptake and low cytochrome oxidase activity are color-coded *black.* Cortical regions where there is both high cytochrome oxidase activity (green) and high DG uptake (red) appear *yellow.* For further details, see Switkes et al. (1986). *A* is taken from an animal that was shown, through one eye, a spatially diffuse visual stimulus that changed continuously from red to gray and back again. The resulting ocular dominance columns are blob-shaped rather than continuous and striplike, and the blob-shaped regions of high DG uptake overlay the cytochrome oxidase blobs within the stimulated eye dominance column. *B* is taken from the same hemisphere as *A,* and is stimulated identically except that in this region of striate cortex, the animal viewed a spatially diffuse stimulus changing from blue to gray, rather than from red to gray. Again, regions of high DG uptake overlay the cytochrome oxidase blobs. The fact that DG uptake is high on all the stimulated cytochrome oxidase blobs (and apparently within all regions of the cytochrome oxidase blobs) in response to red (*A*), blue (*B*), and green (not illustrated) is evidence against the idea of a segregation of cells according to hue/wavelength. In *C,* the animal viewed an equiluminant color grating at systematically varied orientations. The grating stripes were varied between red–green, blue–yellow, and purple–cyan. In resonse to this color grating, DG uptake is highest on the blobs. In response to a black–white grating that is otherwise similar, DG uptake is equally high on the blob and interblob regions at this eccentricity. Calibration bar, 2 mm.


A
B
C

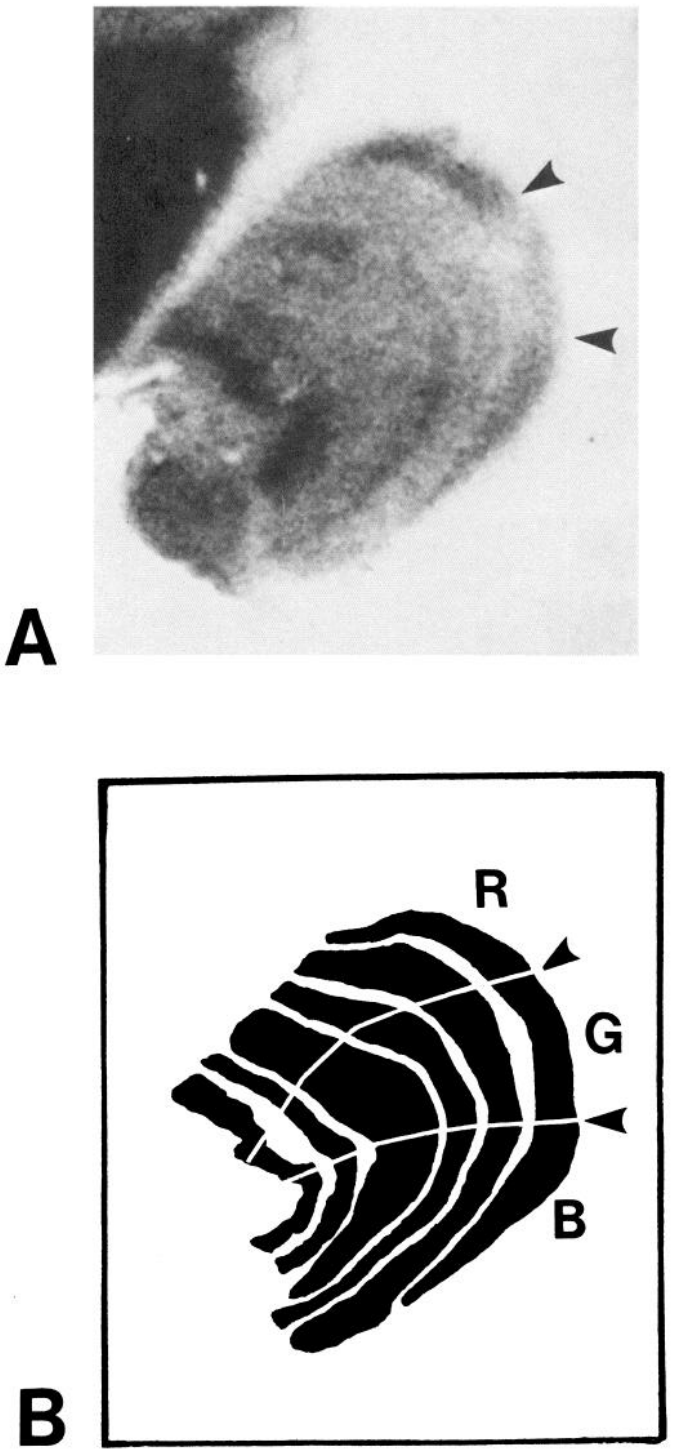


Figure 9. *A*, DG autoradiograph of a coronal section through the LGN in the split-field wavelength comparison described in Figure 6. *B*, Diagram of the 6 geniculate layers in *A*, drawn from the section in *A* after Nissl staining. The 2 *arrowheads* in *A* and *B* (and the *thin white lines* in *B*) indicate the approximate retinotopic borders of the different stimulus wavelength regions. In *B*, the letters indicate the geniculate region stimulated, either with red (*R*), green (*G*), or blue (*B*) versus gray. At least in the parvocellular layers, there is a definite wavelength bias in DG sensitivity. There is no obvious uptake in the intercalated layers. Scale bar, 2.5 mm.

oxidase blobs. However, at this level of DG resolution there is no obvious evidence for such hue columns.

LGN

Because the hue bias was so unexpectedly robust in the striate deoxyglucose results, we naturally wondered whether the bias could also be seen in the LGN, or whether it first appeared within striate cortex. The fact that the hue bias could be seen in striate layer 4C indicated that it might be traced back at least to the principal LGN cells. We therefore sectioned and exposed the contralateral LGN from the case illustrated in Figure 6. As can be seen in Figure 9, different wavelength sectors (equated for luminance and purity) produced different levels of DG uptake in the parvocellular layers of the LGN. As was found in striate cortex, shifts to red and blue produced much more uptake than shifts to green. Thus, although our data base is rather skimpy, it appears that the DG hue bias can be traced back at least as far as the parvocellular LGN layers, and perhaps to the retinal ganglion cell level.

In Figure 9, the level of uptake in the stimulated magnocellular layer is actually darker than that in the stimulated parvocellular layers. This is contrary to the relationship of uptake in geniculorecipient striate layers 4A, 4Ca, and 4Cb, in which uptake is much higher in the parvorecipient (4A and 4Cb) than the magnorecipient (4Ca) layer. It is not clear why this color-specific uptake occurs in the magnocellular LGN layers. It could conceivably be related to the presence of a red-suppressive surround in some magnocellular cells (Wiesel and Hubel, 1966), but this is only conjecture. At any rate, it does not affect the striate cortical input to 4Ca (see Figs. 5, 6).

In the squirrel monkey, a projection to the cytox blobs has been demonstrated from the LGN, and the origin of the projection has been attributed to the supernumerary (intercalated) layers of the LGN (Fitzpatrick et al., 1983). However, this result has not been replicated in the macaque. In those cases stimulated with spatially diffuse color flicker, the color information reaching the cytox blobs might therefore be derived from a direct projection from the supernumerary LGN layers. If this were true, one might expect high DG uptake in the intercalated LGN layers, as well as in the striate cytox blobs, in these cases. In the LGNs from relevant cases that we have sectioned, stimulus-related uptake was obvious in the numbered parvocellular and magnocellular layers, but subtle or absent in the supernumerary ones (see Fig. 9). On the basis of this and other DG evidence, we suggest that, in the macaque, the cytox blobs may not receive significant input from the supernumerary layers. More likely, the cytox blobs receive strong input from the parvocellular LGN layers via 4Cb and 4A (or via the weak direct projection demonstrated by Horton, 1984), in addition to a somewhat weak input from the magnocellular layers via 4Ca.

Grating stimuli

General results

The results from spatially diffuse stimuli are interesting, but the natural world (in which our visual system has evolved) does not consist entirely of large, fuzzy patches of luminance or color. Furthermore, it is well-known that many striate cortical cells have strong spatial tuning and cannot be stimulated with spatially diffuse stimuli, even in the color domain (Dow, 1974; Gouras, 1974; Michael 1978a–c; Thorell et al., 1984). Therefore we did a number of tests to examine the functional anatomy

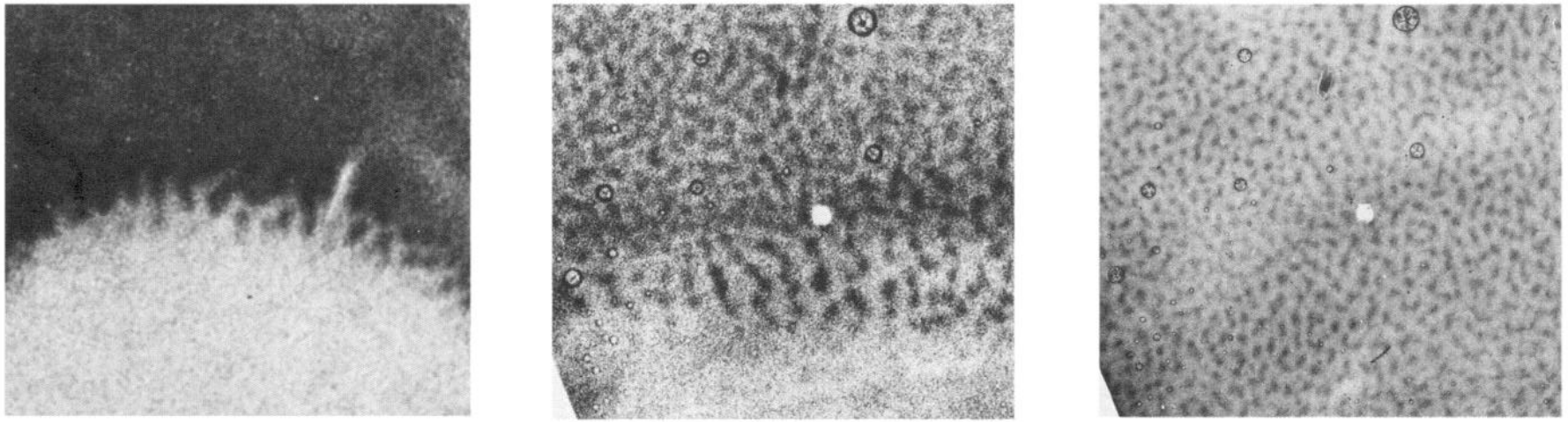


Figure 10. Between-animal comparison of the DG effect of luminance- (*A*) and color-varying (*B*) stimuli. Taken from parafoveal layer 3. The stimulus producing DG uptake in the top half of *A* was a black–white square-wave grating of variable spatial frequency presented binocularly at all orientations. The stimulus for the bottom of *A* was a diffuse gray screen; between the 2 is a thin, monocularly stimulated segment. The stimulus used to produce *B* was identical to that in *A*, except that the grating stripe varied in color (red–cyan, green–purple, and yellow–blue), rather than in luminance. Again, the bottom portion contained an unstimulated and, above that, a monocularly stimulated strip of cortex. The top half of *B* shows the binocularly stimulated region. DG uptake following color stimulation appears much more bloblike. *C*, The cytochrome oxidase blobs in the same section used for the DG autoradiograph in *B*. By comparing *B* and *C* it can be seen that the regions of bloblike high DG uptake following color stimulation are coincident with the cytochrome oxidase blobs; this is verified in Figure 8*C*. Scale bar, 5 mm.

underlying the perception of oriented grating patterns that varied in either color or luminance.

In all, 3 animals (cases 12, 17, 54) were shown colored grating stimuli. Thirty-one monkeys were shown black–white grating stimuli, many in the context of different but related experiments. Another 9 animals were shown split-field stimuli that contained both luminance-varying and color-varying gratings in adjacent portions of the visual field (cases 23, 24, 27, 29, 33, 34, 38, 41, 48, 53).

In an experiment described in detail in the first paper of this series (Tootell et al., 1988a), we stimulated striate cortex binocularly with a black–white square-wave stimulus that was systematically varied in both orientation and spatial frequency; this produced a pattern of DG uptake that was topographically uniform in all layers within the parafoveal representation (case 37). The layer 3 topography of this case is shown in Figure 10*A*. However, in the same regions of the color-varying stimulus cases we have considered so far, DG is taken up maximally in the cytox blobs.

To sort out whether this discrepancy is due to the spatial or spectral differences between stimuli, we presented a monkey with a color-varying stimulus that was otherwise quite similar to the black–white case shown in Figure 10*A* (case 12). The color-varying stimulus was a square-wave grating of 0.5, 1.2, and 3.0 cycles/deg, shown at all orientations (in 45° steps), drifted across the screen at a temporal frequency of 3 Hz (thus, a velocity of 1–6 deg/sec), and changed in direction every 5 sec. The grating was composed to equiluminant color pairs, which were varied systematically between red–cyan, blue–yellow, and green–purple.

The autoradiographic result of this stimulus in layer 3 is shown in Figure 10*B*. It is clearly more spotty than the results produced by the spatially analogous black–white stimulus pattern shown in Figure 10*A*. This spotty pattern of DG uptake was clear-cut at all eccentricities sampled (0–8°). The topography in layers 1, 2, 5, and 6 of the color-varying case was also spotty; corresponding layers of the black–white case were topographically quite uniform in the parafovea. As in the spatially diffuse, color-varying cases, uptake in layer 4Cb was greater than that in 4Ca, and the interblob area of layer 6 took up a little DG.

From the geometry, we suspected that the spotty pattern of DG uptake was highest in the cytochrome oxidase blobs. In order to examine this more carefully, both the DG and cytox patterns from the same section were densitized, aligned, and overlaid (see Figure 8*C*). It can be seen that the correspondence is quite good; the DG in this case is obviously highest in the cytochrome oxidase blobs.

From these comparisons it would appear that color information is channeled preferentially through the parvocellular-input pathways (striate layer 4Cb) and to the extragranular cytox blobs. However, in the extragranular layers, the functional architecture for color and luminance appears to be interrelated with the striate architecture underlying spatial frequency peak sensitivity (Tootell et al., 1982, 1983b), at least at this level of DG resolution. Presumably this is a direct reflection of the electrophysiological finding that the receptive fields of (color) blob cells are several times larger than the (noncolor) receptive fields in the immediately surrounding interblobs (D. H. Hubel and M. S. Livingstone, unpublished observations and personal communication). Color–luminance differences such as those in Figure 10, *A* and *B*, are produced reliably when color- and luminance-varying stimuli that contain either a wide range of spatial frequencies or spatial frequencies over the middle range are presented. Within this spatial frequency range, we have produced several cases in which the color–luminance differences seen between animals (Fig. 9) have been confirmed within a single animal using split-field stimuli of otherwise similar spatial characteristics.

One of the most interesting of these split-field confirmations came from a double experiment that was designed to test for a hue bias (akin to that seen earlier), as well as for differences between luminance- and color-varying stimuli in the middle-spatial-frequency range (case 38). The stimulus used in this experiment was divided up into 4 equal-sized sectors within a circular mask. A 2.7 cycle/deg sine wave was displayed in all sectors at all orientations, and moved across the stimulus screen at a range of velocities in both directions. In 3 of the 4 stimulus sectors, the luminance was held constant and the sine wave corresponded to color modulation between a single hue (either red, green, or blue) and an equiluminant gray. In the fourth sector, a black–white sine wave was presented. One of the animal's eyes was occluded and the other was centered near the middle of the stimulus screen. The stimulus was arranged so that 2 of the sectors (the red–gray and the black–white) were mapped onto both hemispheres and could thus serve as controls for interhemispheric differences in histological processing. The other 2 sectors appeared on a single hemisphere. Thus the effects of 3 sectors appeared on each hemisphere.

Representative sections from one hemisphere of this case are shown in Figure 11. The differences between the hue sectors are quite obvious. However, before considering these, we first wish to point out the color–luminance differences. As one would expect from a comparison between animals (e.g., Fig. 10), the extragranular pattern of DG uptake in response to the luminance-varying grating is quite uniform within an ocular dominance strip, whereas that produced by the red–gray grating is much more spotty. This difference is most obvious towards the fovea, and less so more parafoveally (where a 2.7 cycle/deg grating is effectively at a higher spatial frequency). As analyzed in Figure 8, *A–C*), the spotty regions of high DG uptake in the upper and lower layers produced by the color-varying stimuli are in register with the cytochrome oxidase blobs in the stimulated eye dominance columns.

Hue tests

As in the spatially diffuse cases, the red–gray stimulus is much more effective than the green–gray in causing DG uptake (see Fig. 11). When the stimulus was a grating from the mid-spatial-frequency range, the difference between levels of uptake produced by these 2 wavelengths is prominent in all cortical layers, even in magnocellular-influenced layers 4Ca and 4B (although the DG patterns are much lighter in these layers).

The levels of DG uptake produced by the blue–gray grating in the other hemisphere are similar to those produced by the adjacent red–gray grating. Since the red and blue are almost equally effective in producing DG uptake (and since the green is quite ineffective), it appears that the hue bias described above (using spatially diffuse stimuli) is confirmed in these experiments using spatially-varying chromatic stimuli.

Variations with spatial frequency

As described earlier, there is little attenuation of sensitivity to color-varying stimuli at low spatial frequencies in striate DG results (see Fig. 4 and below), in psychophysical data (Van der

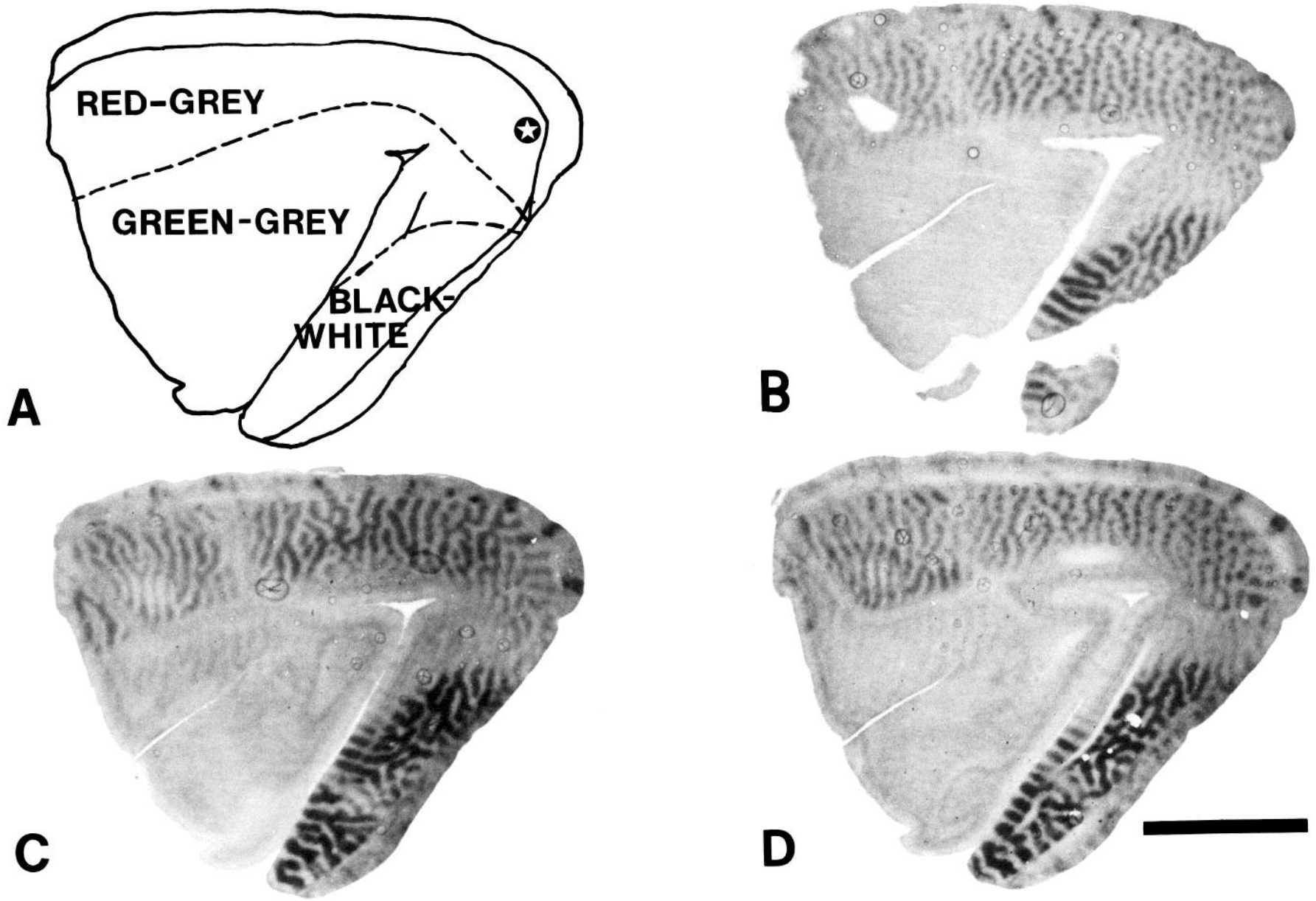


Figure 11. Split-field DG comparison of the effects of different wavelength and luminance combinations in grating stimuli. The animal in this case was stimulated monocularly, presented with a red–gray, a green–gray, and a black–white grating in portions of the visual field corresponding to the top, middle, and lower portion of cortex, respectively. The representation of the stimulus sectors on this hemisphere is shown in *A*. All gratings were sinusoidal, 2.7 cycles/deg, and shown at various orientations. The relative luminance of the red, gray, and green gratings was approximately equal. The sections used in *B–D* were cut from successively deeper layers of a single, flattened operculum. *B* cuts through layer 3, *C* mostly through layer 4, and *D* mostly through layers 5 and 6. As in cases stimulated with spatially diffuse color combinations, long and short wavelengths (such as a red in the red–gray) produce more DG uptake than do middle wavelengths (such as the green), even when combined in a color–gray grating of middle spatial frequency. In the upper (and lower) striate layers, uptake produced by the red–gray color grating is confined to the stimulated cytochrome oxidase blobs, while that produced by the black–white grating fills up both blob and interblob regions within the stimulated ocular dominance strips. This confirms the results from comparisons of black–white and color–gray variations between animals (e.g., Fig. 10). Scale bar, 1 cm.

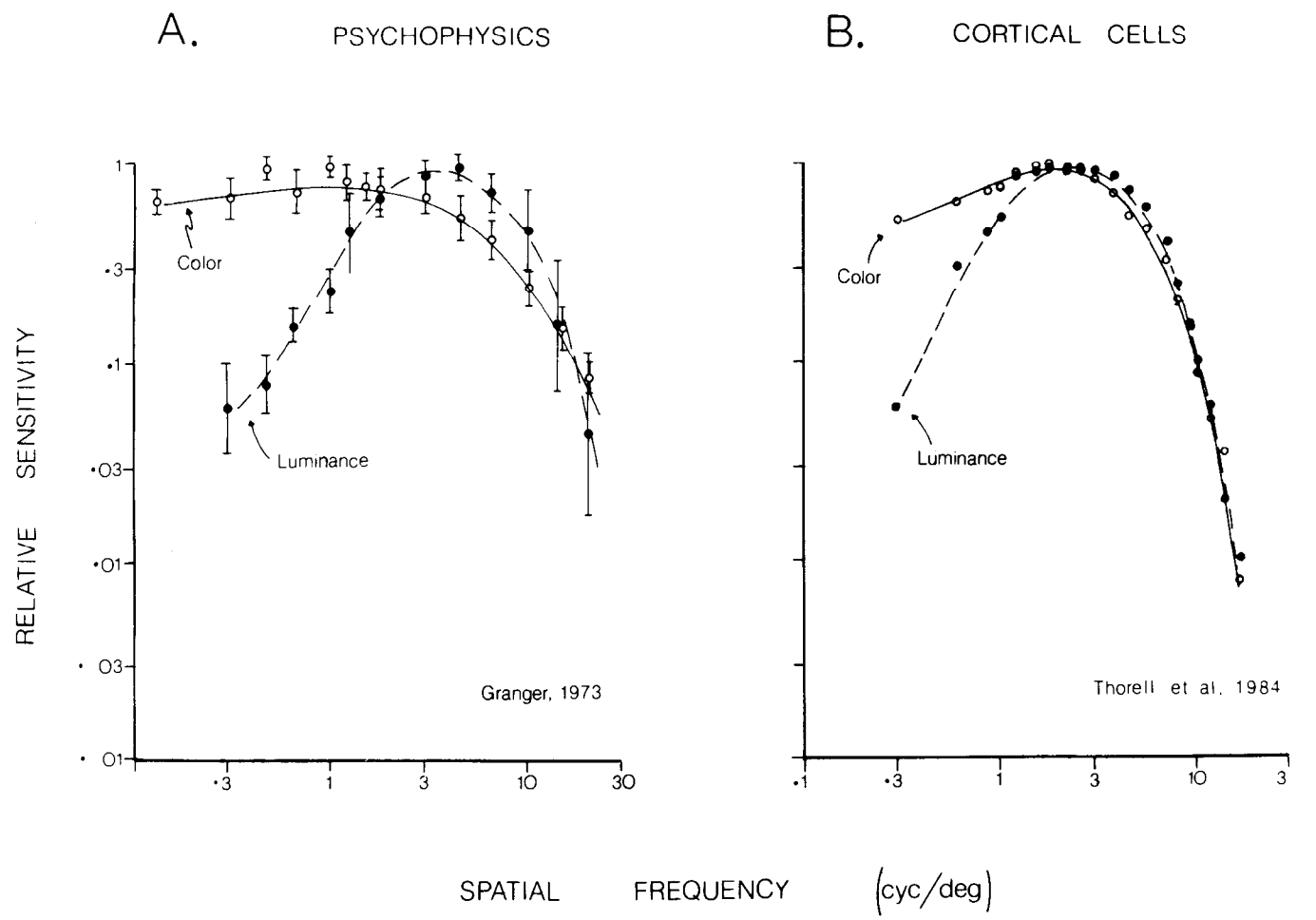


Figure 12. The relationship of psychophysical and physiological measurements of sensitivity to luminance-varying and color-varying gratings across the visible spatial frequency range. The human sensitivity to luminance-varying (*solid circles*) and equiluminant red–green sinusoidal grating (*unfilled circles*) stimuli is reproduced from Granger (1973) in *A*. *B*, Summed responses of 108 striate cells to color- and luminance-varying sinusoidal gratings (*unfilled* and *filled circles*, respectively). The cell data are reproduced from Thorell et al. (1984). For ease of comparison, both curves have been normalized to 1. Both curves show that sensitivity to color-varying (but not luminance-varying) stimuli is relatively high at low spatial frequencies. At high spatial frequencies, sensitivity to luminance-varying stimuli is somewhat higher. Qualitatively, the levels of DG uptake produced by color- and luminance-varying stimuli (at different spatial frequencies) match the results in *A* and *B* quite well.

Horst and Bouman, 1969; Granger and Heurtley, 1973; Watanabe et al., 1976), and in single-unit responses from LGN or striate cortex (see De Valois et al., 1977; Hicks et al., 1983; Thorell et al., 1984).

At middle spatial frequencies, sensitivity in psychophysical color and luminance channels (and in the color and luminance responses of striate cells) is quite high. Thus, it is not surprising to find strong DG uptake in response to both color- and luminance-varying stimuli in the middle-spatial-frequency range (see Fig. 11). In particular, DG uptake in response to the luminance-varying, middle-spatial-frequency grating is very robust; it is, in fact, more robust (at the contrasts we used) than the DG uptake in response to the equiluminant hue–gray gratings. (However, there is of course no *direct* comparability between luminance-varying and color-varying gratings.)

In comparison, recall that spatially diffuse variations along the black–white axis, and the black–white gratings of a very low spatial frequency, produced essentially *no* DG uptake (see Figs. 3, 4). Black–white sine wave gratings of a spatial frequency midway between these 2 extremes (about 1–1.5 cycles/deg) produce DG uptake that is relatively faint but certainly higher than that produced by black–white gratings of even lower spatial frequency. This frequency-dependent shift in DG uptake in response to black–white stimuli is entirely consistent with psychophysical evidence (Van der Horst and Bouman, 1969; Granger and Heurtley, 1973 Watanabe et al., 1976) and with physiological evidence (De Valois et al., 1977; Hicks et al., 1983; Thorell et al., 1984), showing that there is a marked low-spatial-frequency attentuation in response to black–white stimuli (see Fig. 12).

The topography of uptake in the extragranular layers is shifted for color versus luminance stimuli so that DG uptake, at comparable spatial frequencies, is biased more towards the cytox blobs in cases stimulated with color. According to these 2 general predictions about the level and topography of DG uptake, an equiluminant high-spatial-frequency color grating should produce (1) lower uptake than a luminance grating at the same (high) spatial frequency (see Fig. 12), and (2) a topography in parafoveal layer 3 uptake that is more uniform than the characteristic high *interblob* uptake produced by high-spatial-frequency luminance gratings.

We tested both predictions in 2 animals. To test whether a

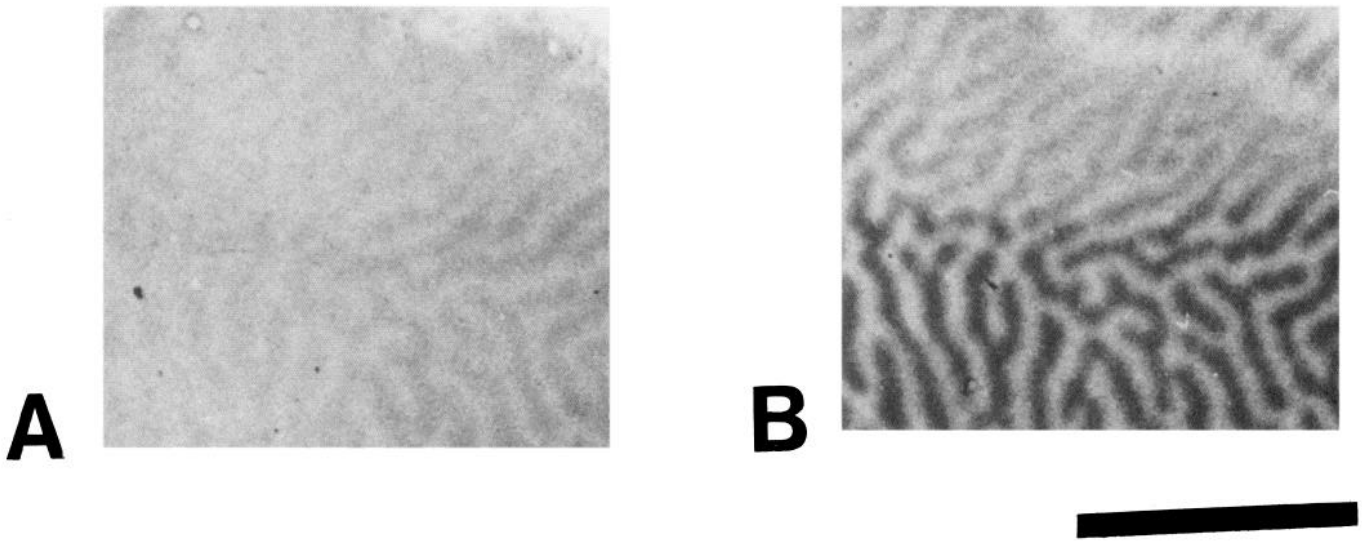


Figure 13. Split-field DG comparison of the effects of an equiluminant red–gray versus an isochromatic, luminance-varying red–black grating, when both are at a high spatial frequency. In this case, a monkey was monocularly presented with a 6.5 cycle/deg grating at all orientations, in a red–gray and a red–black sector separated along the horizontal meridian. Results from that border region are shown from topographically corresponding regions of parafoveal layer 3 (*A*) and layer 4C (*B*). The red–gray sector appears in the top half of *A* and *B*, and the red–black in the bottom half. The red–black sector is obviously more effective in causing DG uptake. Scale bar, 5 mm.

high-spatial-frequency color grating would produce less uptake than a luminance-varying grating containing the same frequencies, we presented one monkey with a split-field stimulus (case 53). In both halves of this stimulus, a grating of 6.5 cycles/deg was shown at all orientations, and moved within a range of velocities in a direction that changed every 5 sec. The stimulus was split along the horizontal meridian. In the bottom half, the grating was an equiluminant red–gray; an isochromatic red–black grating appeared in the top half. The animal was stimulated monocularly through an eye that was centered on the horizontal stimulus meridian.

The results from parafoveal layer 3 of this case are shown in Figure 13. Cortical regions stimulated by the red–gray grating are represented in the uppermost half of Figure 12, and regions stimulated by the red–black are below. The luminance-varying (red–black) grating clearly produces more uptake, especially in layer 4Cb (see Fig. 13).

To further examine the topography of DG uptake produced by a 6.5 cycle/deg red–gray grating, we stimulated another animal binocularly (case 54). The grating in this case was presented at all orientations, and moved across the screen at a range of temporal frequencies. In other animals, a 6.5 cycle/deg luminance-varying grating has been found to produce a characteristic annular pattern of high uptake between the cytox blobs in parafoveal layer 3 (Tootell et al., 1982, 1983b).

In the present case, the red–gray grating produced a pattern of uptake at the same cortical eccentricity that was topographically uniform in all layers, including layer 3 (see Fig. 14). It was possible to confirm that the uniform pattern of DG uptake was stimulus-driven (rather than endogenous) by noting the presence of (1) a stimulated–unstimulated border in V1 on the underside of the operculum, at the representation of eccentricities that were more peripheral than those shown in Figure 14; and (2) very obvious stimulus-driven DG periodicities in area V2 throughout the representation of relevant eccentricities in V1. Thus, the generality that color-varying stimulation produces a shift towards the cytox blobs (relative to luminance-varying stimuli at comparable spatial frequencies) seems to hold for high spatial frequencies, as well as for the other frequency ranges studied. Nearer the fovea, relative levels of uptake were higher in the cytox blobs, which was also to be expected. As was the case in the experiment shown in Figure 13, the DG contrast produced by the color-varying grating was somewhat lower than that produced by a comparable luminance-varying grating.

Color–luminance laminar differences

Across a wide variety of spatial configurations, color- and luminance-varying stimuli produce somewhat different levels of DG uptake in different laminae. This difference is most striking in split-field comparisons of luminance- and color-varying stimuli in which all other relevant visual parameters are varied equally. One clear example is an experiment in which an animal was shown a square-wave grating of varied spatial frequency (0.8, 1.8, and 4 cycles/deg) at 4 different orientations (in 45° steps) drifted across the visual field at a temporal frequency of 2–5 Hz (velocity range, 0.5–6 deg/sec), and reversed in direction every 5 sec (case 23). In the top half of the visual stimulus, the grating was made up of equiluminant red–green stripes, and in the bottom half of the screen, of black–white stripes. The foveal projection of one eye was positioned at the center of the screen, and the other eye was occluded.

Levels of uptake in the color- and luminance-varying cortical regions were measured in each layer: the results are shown in Figure 15. In layers 1, 2, 3, 4A, 4Cb, 5, and 6 of this case, stimulus-related levels of DG uptake in the color-varying region are only slightly lower than those in the luminance-varying region. However, in layers 4Ca and 4B, there is a striking decrease in DG uptake in the color-varying portion of striate relative to the luminance-varying portion and to other layers of the color-varying portion. The strong difference between uptake in the parvocellular-influenced layers (such as 4Cb) and that in the magnocellular-influenced layers (4Ca and 4B) is most compel-

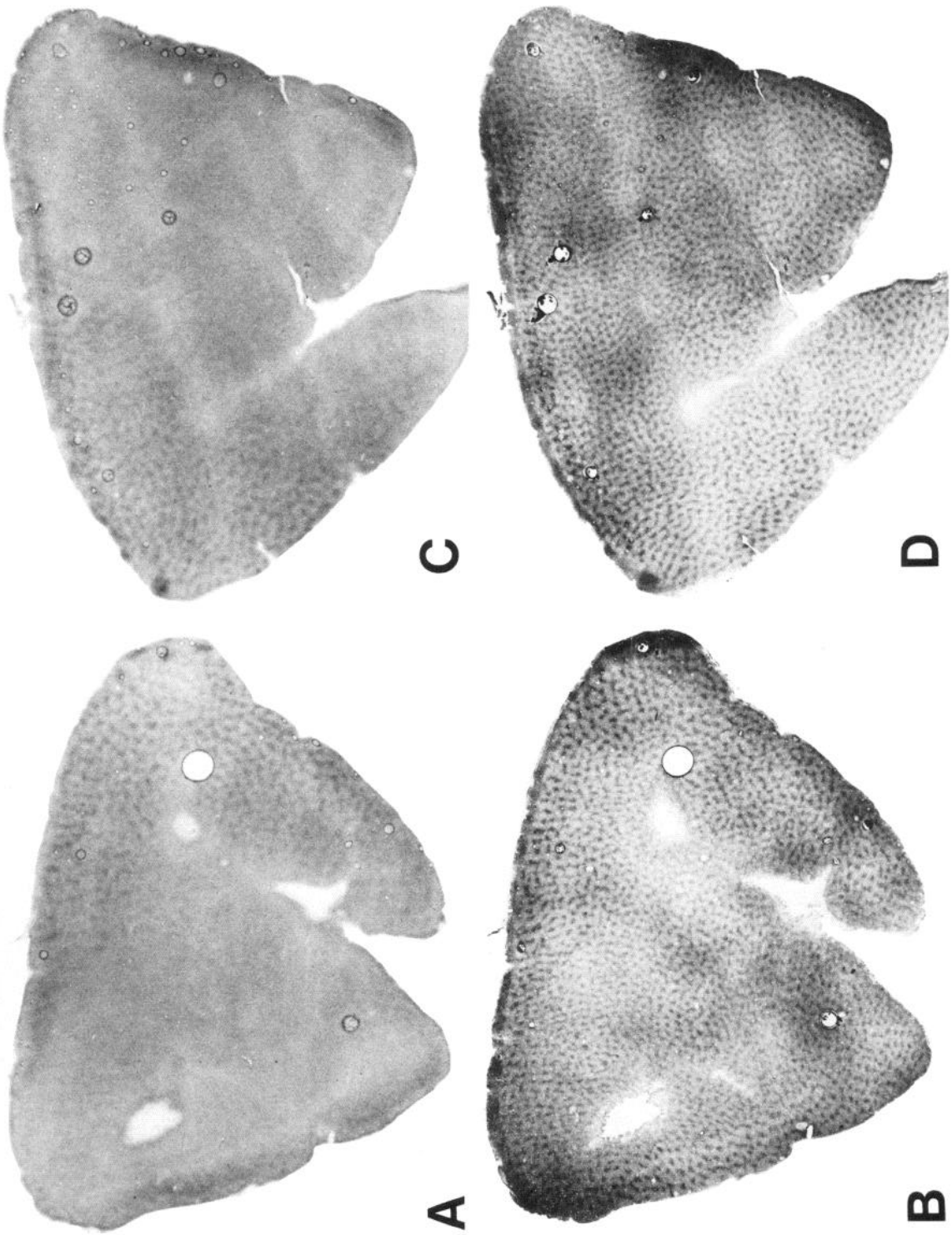


Figure 14. Overall DG topography produced by a high- (6.5 cycles/deg) spatial-frequency red–gray grating presented binocularly at all orientations. *A*, *C*, DG topography of one layer 3 section from each flattened operculum. For comparison, *B* and *D* show the same sections after staining for cytochrome oxidase. The striate foveal representations are closest to the middle; more peripheral eccentricities appear towards the right and left. Such a stimulus produces a relatively light pattern of DG uptake, which is high in the foveal blobs and topographically uniform more peripherally. Various controls (see text) indicate that the uniform pattern of parafoveal layer 3 uptake is stimulus-driven and well above visually unstimulated levels. Scale bar, 1 cm.

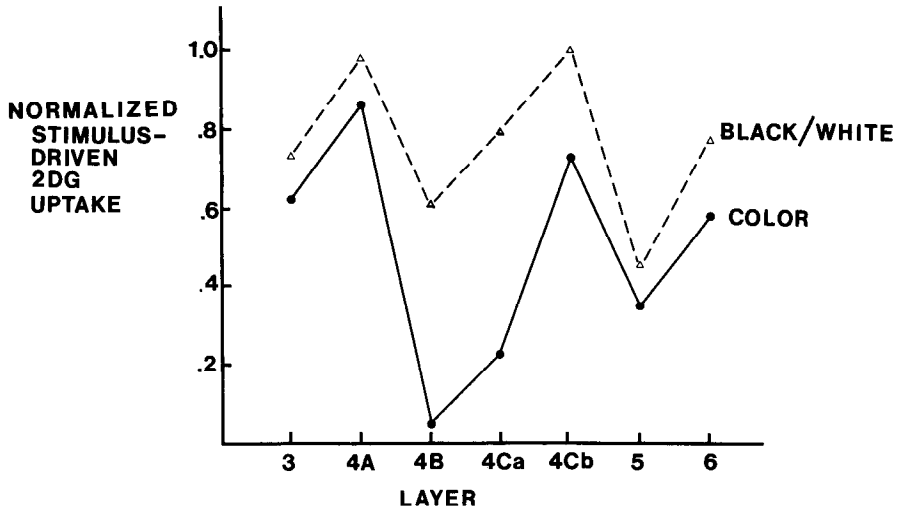


Figure 15. Denisitometric analysis of DG uptake produced by a luminance-varying (*unfilled triangles*) and a color-varying (*filled circles*) grating within a single hemisphere. Both gratings were systematically varied in orientation and spatial frequency, and separated from each other along the horizontal meridian. The stimulus was presented monocularly, and the gratings were set to the same mean luminance. The color-varying grating was varied between red–cyan, blue–yellow, and green–purple. In each layer for each grating representation, 30–50 samples of the autoradiographic density were taken through an aperture of 25 × 25 μm, centered over the darkest (stimulus-related) and lightest (stimulus-unrelated) regions. Both averaged densities were converted to levels of uptake via radiographic standards, and stimulus-unrelated uptake was subtracted from uptake in the darkest regions to yield a measure of stimulus-driven uptake. In most layers, stimulus-driven uptake produced by the color grating is only slightly less than that produced by the black–white grating. However, in layers 4B and 4Ca (which are influenced predominantly by the magnocellular layers), the color gratings produce very little uptake. This is cognate with reports that color sensitivity is low in the magnocellular layers and cortical area MT (to which layer 4B projects).

ling in autoradiographs of the color–luminance border region (see Fig. 15). The laminar differences described in Figures 15 and 16 are similar to those reported by Crawford et al. (1982) between color- and luminance-varying orientation columns of different animals.

Tests of double-opponency

Livingstone and Hubel (1984a) have reported that about half of the cells in the upper-layer cytox blobs are double-opponent color cells. This kind of cell will respond well to color gratings of the appropriate spatial frequency, but poorly or not at all to spatially diffuse color variations or to color gratings of very low spatial frequency (<0.5 cycle/deg in foveal and parafoveal representations) (Thorell et al., 1984). However, spatially diffuse color variations, and color gratings in the very low to medium (that is, up to 3–4 cycles/deg) spatial frequency range, do produce high DG uptake in the cytox blobs.

The high DG uptake that is produced in the cytox blobs by spatially diffuse color stimuli could not be produced by the action potentials from double-opponent color cells with well-balanced surrounds. However, it could be due to activity in the single-opponent color cells in the cytox blobs or in double-opponent cells with weak surrounds; both these cell types are also found in the cytox blobs (Livingstone and Hubel, 1984b). (Presumably there is a continuum between single- and double-opponent cells, rather than a strict dichotomy.) A less obvious possibility is that the high uptake in the cytox blobs in response to spatially diffuse color patterns might be due to high synaptic activity from (presumptive) single-opponent afferents synapsing on the cytox blob cells, which is nullified at the level of the postsynaptic cell body (recorded electrophysiologically).

No matter which of these interpretations is correct, the reported prevalence of double-opponent cells in the cytox blobs (and the lack of cells responding best to spatially diffuse patterns) means that color gratings of appropriate spatial frequency should produce more DG uptake in the cytox blobs than do spatially diffuse stimuli.

In qualitative comparisons between animals, this assumption seemed to hold up. In the spatially diffuse cases, DG uptake in the upper-layer cytox blobs was less than that in layer 4Cb, whereas in cases stimulated by mid-frequency color gratings, levels of uptake in the cytox blobs was approximately equal to that in 4Cb. [In this comparison between animals, we assume that the predominantly single-opponent layer 4Cb cells and their afferents take up roughly equal amounts of DG in response to both spatially diffuse (very low spatial frequency) and mid-frequency color-varying grating stimuli. Thus, the levels of uptake in 4Cb furnish a reference condition for levels of uptake in the cytox blobs in different animals.]

Obviously, it would be more definitive to make these comparisons of DG uptake in the same animals, so we did a split-field experiment to find out exactly where "double-opponent" DG activity occurs (case 48). In this experiment, the stimulus was divided into 3 sectors per hemifield, so that red–gray gratings of 0.1, 2, and 4.4 cycles/deg appeared in separate sectors of each hemisphere. The gratings were shown at all orientations, and the animal viewed the screen monocularly. The grating of lowest spatial frequency (0.1 cycle/deg) was essentially equivalent to a spatially diffuse, temporally modulated color variation across even the largest striate receptive fields. Each grating moved across a given portion of the stimulus at 3 Hz.

The results from layer 3 of this case are shown in Figure 17. There is clearly more DG uptake in the layer 3 cytox blobs in response to the 2 and 4.4 cycle/deg color gratings than to the more spatially diffuse-field (0.1 cycle/deg) color variations. Thus, in this case there is a concordance of answers from the DG and the electrophysiological mapping approaches. Both techniques indicate that neural activity in the cytox blobs is highly sensitive

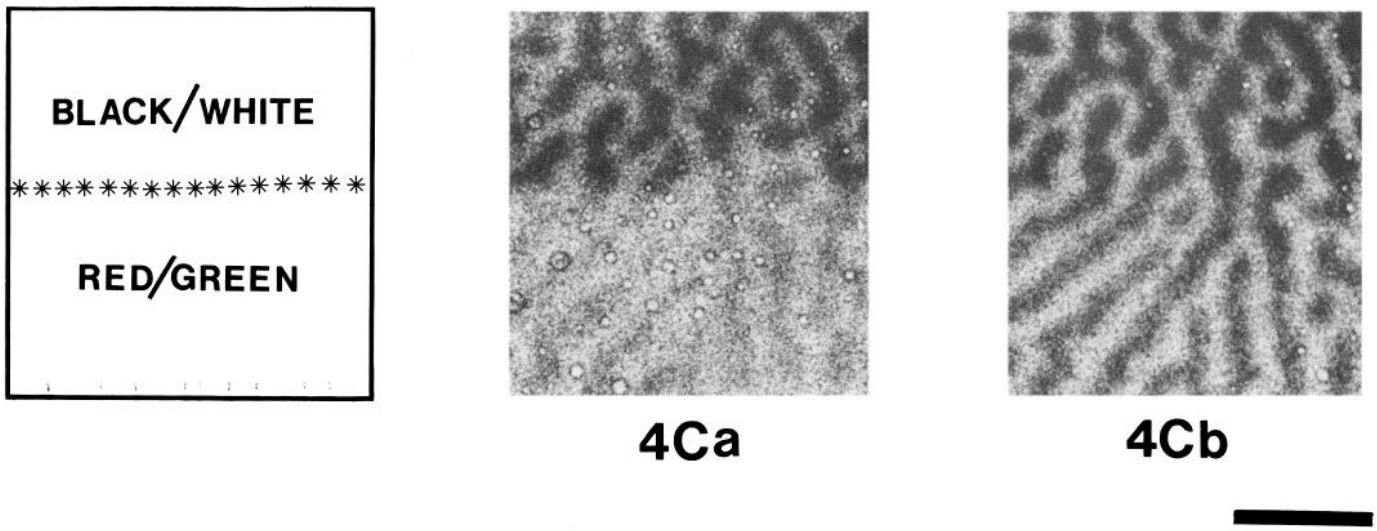


Figure 16. Split-field comparison of the effects of color- and luminance-varying stimuli in corresponding topographical portions of the striate parvorecipient (4Cb) and magnorecipient (4Ca) layers. The stimulus in this case was a square-wave grating varying in either luminance (*top half*) or color (*bottom half*), presented monocularly at systematically varied orientations. Although color and luminance variations are almost equally effective in producing DG uptake in the parvocellular-influenced layer 4Cb and in other striate layers, the magnocellular-influenced layers 4B and 4Ca are quite insensitive to color variations. Scale bar, 2.5 mm.

to variations in color, and both provide persuasive evidence for strong receptive-field surrounds, such as those in double-opponent cells.

Our assumptions about DG activity in layer 4Cb were also borne out: the level of 4Cb uptake was equal irrespective of whether it was produced by diffuse-field variations or by mid-spatial-frequency gratings. This is exactly what one would predict from electrophysiological reports that receptive fields (and LGN afferents) in layer 4Cb are small, single-opponent, and color-sensitive in nature (Blasdel and Lund, 1983; Blasdel and Fitzpatrick, 1984; Livingstone and Hubel, 1984a). The DG results in layer 4Cb provide no evidence for the presence of double-opponent cells in this layer (as described by Michael, 1978b, 1985). By the simplest assumptions, uptake produced by the 0.1 cycle/deg grating corresponds to the activity of center-only color, single-opponent cell processes, and uptake produced by the 2 and 4.4 cycle/deg gratings corresponds to activity in the single- *and* double-opponent cell processes.

We mentioned earlier that it would be interesting to know whether the lower-layer cytox blobs were color-sensitive, and, if so, whether their receptive fields had a double-opponent receptive-field structure. The DG results we have obtained (Figs. 15, 17) indicate that both the upper- and lower-layer cytox blobs take up essentially equal levels of DG in response to color-varying stimuli; by the simplest of assumptions, the lower-layer blobs should be just as color-sensitive as the upper-layer blobs. In the case illustrated in Figure 17, we could also examine the lower-layer cytox blobs for DG evidence of "double-opponency" (given the working assumptions) simply by comparing uptake levels in the diffuse-field- (0.1 cycle/deg) and mid-spatial-frequency (2 and 4 cycle/deg) cases in layers 5 and 6. Granted these assumptions, we see almost as much evidence for double-opponency in layer 5 as in layers 2 and 3. By the same criteria, we see no evidence of double-opponency in layer 6 (see Fig. 17). It will be interesting to see whether future electrophysiological mapping studies arrive at the same conclusions.

Variations with eccentricity

One aspect of the data that deserves mention is the *lack* of variation with eccentricity in the contrast of the autoradiographs from color-varying cases. In the retina, the distance between adjacent cones is smallest in the fovea and increases sharply towards the periphery—the intercone separation at 6° eccentricity is about twice that found within the fovea (Osterberg, 1935; Rolls and Cowey, 1970). The slope of the change in striate cortical magnification with eccentricity is much steeper: in our own DG measurements, the cortical magnification at 6° is only about 19% of that at the foveal representation. From this retinostriate magnification mismatch, one might well expect a variation in the contrast of color-varying DG patterns with eccentricity, since the cones mediate color vision. However, this does not occur; levels of DG uptake within a given layer are quite uniform within the central 8° or so when produced by a wide variety of color-varying stimuli (see Figs. 2, 5, 6).

Although the density of medium- and long-wavelength cones is highest in the fovea, the short-wavelength (S, or "blue") cones are systematically absent within the central 15′ of fovea and rare within the central 30′ (e.g., de Monasterio et al., 1981, 1985). Because the retinotopic projection is so orderly in striate cortex, it is possible that visual stimuli that preferentially activate the S cones create a small area of low uptake in the foveal striate DG patterns. In fact, the blue–gray stimulus variations we used lie quite close to the tritanopic confusion axis, and so this stimulus probably activates the S cones preferentially (although S-cone activity was certainly not completely isolated). We looked for a region of decreased DG contrast in the striate representation of the central 15–30′ in cases in which the animal viewed blue–gray stimuli. These included spatially diffuse stimuli in which blue and gray were modulated across the whole screen or within hue-specific sectors, and for a 2.7 cycle/deg blue–gray sinusoidal grating. No convincing foveal decrease was seen in any striate layer. Though this negative result might in-

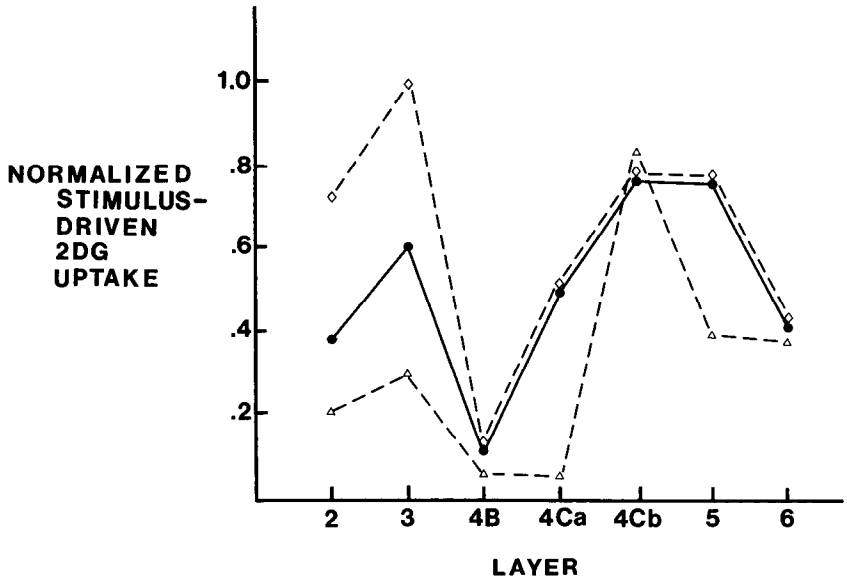


Figure 17. Densitometric analysis of spatial tuning in color cells of different layers. In this case, a monkey was shown a split-field stimulus in which a red–gray grating of either 0.1 (*unfilled triangles*), 2 (*unfilled diamonds*), or 4.4 (*filled circles*) cycles/deg appeared in one of 3 stimulus sectors. The gratings in each sector were systematically varied in orientation and presented monocularly on one-half of the vertical meridian, so that they all were represented within a single hemisphere. Stimulus-driven uptake at each point was measured as described in Figure 15; it was highest in (and thus sampled from) the blobs. The presence of significant spatial tuning (such as that in double-opponent cells) will presumably decrease uptake to sinusoidal gratings of extremely low spatial frequency, such as that indicated by the unfilled triangles. In layers 4Cb, 4B, and 6, there is very little difference between the uptake produced by the gratings of different spatial frequency. In layers 4Cb and 6, this presumably indicates that the receptive fields of color cells are predominantly single-opponent. In layer 4B, the comparison between the effects of different spatial frequencies is meaningless because of a uniformly low sensitivity to color variations in this magnocellular-influenced layer. In all other layers, there is some evidence for significant spatial tuning in color-responsive cells, such as that seen in color double-opponent cells. The DG evidence thus supports the presence of double-opponent color cells in the blobs within layers 2, 3, 5, and 6.

dicate the presence of a foveal "fill-in" process for the S-cone pathway, it is also possible that our stimulus simply did not isolate S-cone activity adequately.

Discussion

Speculation about differences in color and luminance sensitivity at very low spatial frequencies

One of the striking findings that emerged from our studies is that spatially diffuse variations in (some) colors produce strong uptake in striate cortex, while spatially diffuse variations in luminance produce very little uptake at all. This difference between the effects of color- and luminance-varying stimuli occurs either following the use of drifting sinusoidal gratings of very low spatial frequency or when the entire stimulus screen changes temporally in either color or luminance. The presence of a low-spatial-frequency attenuation in the luminance (but not the color) DG results is presaged by numerous psychophysical (Van der Horst and Bouman, 1969; Granger and Heurtley, 1973; Watanabe et al., 1976) and physiological (De Valois et al., 1977; Hicks et al., 1983; Thorell et al., 1984) results showing a similar difference in contrast sensitivities in the color and luminance systems at low spatial frequencies (see Fig. 11).

This difference between color and luminance processing is presumably mediated by single-opponent color cells. Such cells are found in a number of striate regions, including the cytox blobs (e.g., Livingstone and Hubel, 1984a). Because the receptive fields of these cells receive spatially coextensive input from different cone types, they will respond to spatially diffuse, temporal variations in color, as well as to color-varying stimuli of higher spatial frequency. Furthermore, the receptive-field size of such cells appears to be within the same general range as that of neighboring cell types. Thus, activation of the single-opponent color cells will presumably produce a retinotopically discrete DG pattern at the striate representation of the spatially diffuse stimulus borders, as is seen in the data (see Fig. 4).

We were particularly interested in knowing the type of single-opponent cell in the upper-layer blobs, since the upper-layer blobs appear to be the primary source of color information projecting to extrastriate cortex. The predominant type of single-opponent cell in the upper-layer blobs appears so far to be of the center-only (type 1) variety (Livingstone and Hubel, 1984a).

However, double-opponent cells are apparently also found in the upper-layer blobs (Livingstone and Hubel, 1984a). The increased DG uptake we see in response to spatially diffuse color variations could not be produced by the output of color double-opponent cells because well-balanced color double-opponent cells will not respond to spatially diffuse variations in color. Although it is conceivable that the increased blob uptake could be produced by hypothetical single-opponent synapses on the dendrites of double-opponent cells in the blobs, this appears unlikely on the basis of other DG data (see Fig. 17 and below).

The obvious difference in the spatial filtering of color- and luminance-varying stimuli at low spatial frequencies must have some meaning for the functioning visual system. We suggest that the low-spatial-frequency color information in striate cortex is carried passively by the center-only color-opponent cells through striate cortex (and out through the cytox blobs) on its way to V2, V4, IT, or some related extrastriate area, where it can finally be combined in a computation of color constancy.

Color constancy must be attributed to cortical areas beyond

striate cortex for a very simple reason. Color constancy is achieved by integrating color information from the whole of the visual field, and striate receptive fields (of all types) are very much smaller than that. Even the widest-ranging horizontal interconnections in striate cortex serve only a miniscule fraction of the visual area over which color constancy operates. On the other hand, receptive fields (and intracortical connections) become progressively larger throughout extrastriate cortex, some serving much of the visual field in the higher-order areas. Many of these larger receptive cells are also color-responsive in certain extrastriate areas (e.g., V2, V4, IT). There is some evidence from both lesion and single-unit studies to support the idea that color constancy is mediated in V4, or in some area to which V4 projects (Zeki, 1980; Wild et al., 1985). Therefore, it seems most logical to attribute the computation of color constancy to extrastriate areas with demonstrable color sensitivity and large receptive fields, such as V4 and IT.

Deoxyglucose experiments using spatially diffuse flicker also show that single-opponent (low-pass) color information (of a type that seems appropriate for color-constancy computation) does in fact get all the way through extrastriate cortex. Spatially diffuse variations in color (but not luminance) produce discrete regions of very high DG uptake in a number of extrastriate regions, including V2, V4, and IT (Tootell et al., 1980). If color constancy were achieved *within* striate cortex, spatially diffuse variations in color should produce no increase in DG uptake in areas beyond striate cortex because this information would presumably be nulled out in the constancy computation within striate cortex. So it is clear that information about average wavelength composition within a large region of the visual field (of the type needed to compute color constancy) is available to visual cortical areas well beyond striate cortex, even when the color information is presented within a spatially diffuse context. Of course, the color information reaching V4, IT, and associated areas passes through the upper striate layers and V2 first, so we may assume that one function of the single-opponent color cells in the upper-layer cytox blobs could be to passively carry forward the spatially primitive information about average wavelength through the various primary regions into extrastriate cortex.

One complication to this general idea is that brightness constancy is similar in certain respects to color constancy, and, by the present model, we would need to postulate that the computation of brightness constancy occurs at very different (precortical) levels than does the color-constancy computation. It is necessary to assume that brightness constancy is computed prior to striate cortex, because large, diffuse black–white variations in luminance (brightness) produce little or no DG uptake in or beyond striate cortex and insignificant response in striate single units (e.g., Thorell et al., 1984). Spatially diffuse black–white variations will often produce responses in LGN and retinal ganglion cells, however.

Laminar distribution of single- and double-opponent color cells

Since double-opponent cells do not appear in the primate at levels prior to striate cortex (e.g., Wiesel and Hubel, 1966; De Valois et al., 1977; Schiller and Malpeli, 1978), another function of the single-opponent cells (at some level) must be to furnish the information necessary to wire up color double-opponent receptive fields.

It has been suggested that color double-opponent receptive fields first appear at the level of striate layer 4Cb (Michael, 1978b), and that this double-opponent information is then relayed to double-opponent cells in the overlying cytochrome oxidase blobs (Michael, 1985). Alternatively, it has been suggested that color double-opponent receptive fields are seen only rarely, or not at all, in striate layer 4Cb (Blasdel and Lund, 1983; Livingstone and Hubel, 1984a), and that they appear first in the cytox blobs themselves (Livingstone and Hubel, 1984a).

Since cells with double-opponent receptive fields will not respond to color gratings of very low spatial frequency (Thorell et al.,1984), it proved possible to discriminate single- from double-opponent-type activity in split-field DG experiments (see Fig. 16). In such tests we see clear evidence for double-opponent color responses in the layers 2 + 3 cytox blobs, but no evidence for double-opponency in layer 4Cb. On the face of it, this supports the laminar picture drawn by Livingstone and Hubel (1984b), to the exclusion of that drawn by Michael (1978b).

However (as usual), it may be slightly more complicated than that. It is not yet clear to what extent the DG in our experiments reflects uptake into cell bodies, and to what extent it represents uptake into neuropil (see discussion in Tootell et al., 1988a). Therefore, it could be argued that the DG evidence against color double-opponency in layer 4Cb reflects only the activity of single-opponent parvocellular inputs and synaptic interactions prior to the axon hillock of (presumptive) double-opponent cells in layer 4Cb. We cannot rule out this possibility, but it seems unlikely that double-opponency in a significant proportion of layer 4Cb cells would fail to contribute to the overall DG uptake in that layer. Furthermore, the small variation in our DG measurements in layer 4Cb, the split-field experimental context, and the obvious DG evidence for double-opponency in the upper-layer cytox blobs all argue strongly for an actual lack of double-opponency in layer 4Cb.

The DG evidence for color double-opponency in the layer 2 + 3 cytox blobs is interesting on several levels. For one thing, it is one additional instance of a concordance between electrophysiological (Livingstone and Hubel, 1984a) and DG measurements. To see how far the concordance between DG and electrophysiological results can be pushed, it is interesting to compare the levels of "single-opponent" and "double-opponent" DG uptake in the cytox blobs (Fig. 17) with the percentage of such cells in previous electrophysiological studies. Livingstone and Hubel (1984a) classified about a third of the non-oriented (blob) cells as center-only single-opponent, and the other two-thirds as double-opponent. In Figure 17, the stimulus-related uptake we ascribe to single-opponent activity (that is, that in the 0.1 cycle/deg sector of cortex), is about a third as high as that which can be described as single- plus double-opponent (that in the 2 and 4 cycles/deg sectors). Although there is no compelling reason to expect an exactly linear relationship between the number of units in a certain single-unit class and the level of DG uptake produced by that class, the correlation works out nicely in this case.

On the other hand, it is disappointing in some ways that a well-defined discrepancy between DG and single-unit measures has not yet been found. For instance, if we had found no DG evidence for double-opponency in the blobs, this could be construed as being due to a heavy innervation of the dendrites of blob cells by single-opponent inputs. Such a result could be reflected by the DG affinity for neuropil, but be invisible at the level of the single-unit electrode sampling activity from the blob cell body. [A similar interpretation could yet rationalize the

reports of color double-opponent cells in layer 4Cb (Michael, 1978b, 1985) with the complete lack of DG evidence for such activity.] The point here is that when such a "discrepancy" between the DG and single-unit techniques can be found, it could eventually shed more light on the underlying neural circuitry than a simple concordance of results could ever do.

The lower-layer cytox blobs stain only very lightly for cytochrome oxidase (Horton, 1984; Livingstone and Hubel, 1984a; see also Tootell et al., 1988a). However, color-varying visual stimuli from the low- and middle-spatial-frequency range produce high DG uptake in both the upper- and the lower-layer blobs (see Figs. 1, 2, 6). The high contrast of the lower-layer DG blobs makes it more likely that a parcellation of function exists in the lower layers, analogous to that in the upper layers.

One obvious question concerns the types of cells found in the lower-layer cytox blobs and interblob regions. From the DG results, one would expect them to be very similar to cells in the upper-layer cytox blob and interblob regions (respectively), at least in layer 5. Specifically, there should be nonoriented double-opponent color responses in the layer 5 blobs and nonoriented single-opponent color responses in layer 6 blobs. However, the lower-layer cells project to subcortical nuclei, and the upper-layer cytox blobs project forward to extrastriate cortex (e.g., Lund et al., 1976). On this basis, one would expect more functional differences between cells in the sub- and supragranular cytox blobs. An electrophysiological mapping experiment will be necessary to resolve these questions.

As for the anatomical problem of precisely defining the position of the lower-layer cytox blobs, it is worth emphasizing that DG, coupled with spatially diffuse red or blue stimulation, is probably the best technique currently available for labeling the lower-layer cytox blobs. Recent improvements in the resolution and aqueous insolubility of some 2-deoxyglucose metabolites should expand the potential usefulness of this approach (e.g., Sejnowski et al., 1980; Watanabe et al., 1980; Pilgrim and Wagner, 1981; Penreath et al., 1982).

Color and luminance information and functional streams

In cases stimulated with spatially diffuse color variations, stimulus-related DG uptake is very low in both layers 4Ca and 4B (see Figs. 2, 17). However, since spatially diffuse black–white (luminance-varying) stimuli produce little or no DG uptake in *any* layer, it is impossible to compare color- and luminance-varying DG uptake in layers 4Ca and 4B (or in any other layer) meaningfully in cases stimulated with spatially diffuse stimuli.

The fact that DG uptake was light in layers 4Ca and 4B when produced by color-varying (but not luminance-varying) grating stimuli of middle spatial frequency (Figs. 15, 17) supports the wider generality that striate layers 4B and 4Ca are insensitive to color variation per se across a variety of spatial contexts. In our DG results, layers 4Ca and 4B are very sensitive to variations in luminance (see Figs. 15, 16); thus we know that DG uptake in these layers can be robust, given the appropriate stimulus.

The lack of color sensitivity in layers 4B and 4Ca is particularly interesting because of the special relationship of these layers to each other and to their input and output targets. Layer 4Ca receives a major input from the magnocellular layers of the LGN, in which color sensitivity is weak (Blasdel and Lund, 1983; Livingstone and Hubel, 1984b). Layer 4B derives predominant input from layer 4Ca (Lund and Boothe, 1975), and in turn the cells of layer 4B project to area MT (Lund et al., 1976), where color sensitivity is reportedly absent altogether (e.g., Zeki, 1978). In short, it appears that a circuit of color-insensitive information can be traced from the output of the magnocellular LGN layers through striate cortex and finally into area MT.

On the basis of DG data from the present study, as well as electrophysiological and tract-tracing data in other studies (e.g., Livingstone and Hubel, 1984b; De Yoe and Van Essen, 1985; Shipp and Zeki, 1985), it appears that color information travels mainly from the parvocellular LGN layers through striate layer 4Cb to striate layers 2 + 3 (mostly in the blobs), and from there into area V2 (mostly in the thin strips) and into V4 and beyond.

Differential DG response to different wavelengths

One of the strongest (and most unexpected) of the DG effects discovered in this study is a differential responsiveness to various wavelengths. When paired against an equiluminant gray (in either a drifting grating or spatially diffuse flicker), long and short wavelengths (reds and blues) produce robust DG uptake, and middle wavelengths (yellows and greens) produce little or no uptake. This result has been confirmed with the use of grating stimuli and spatially diffuse stimuli, and by equating both stimuli for spectral purity as well as for luminance.

The middle-wavelength (yellow and green) region is the least saturated portion of the spectrum, and the extremes (the reds and blues) the most saturated. Because the saturation differences between individual spectral regions were qualitatively similar to the amount of DG uptake, a psychoanatomical experiment was carried out to test whether equating the various colors for saturation would produce correspondingly equal levels of DG uptake of these stimuli. However, it was found that, even when stimuli of different wavelengths were equated for saturation (as, for instance, when a 35% red–65% white was set adjacent to an almost-pure green), the reds and blues still produced more uptake than the green (see Fig. 7). Though this does not mean that saturation and the DG wavelength bias are necessarily unrelated, it does rule out a simple relationship between the psychophysics and levels of DG uptake.

The presumed relationship between saturation and the DG color bias may be just a wild deoxyglucose chase. However, the hue bias in the DG data does not appear to be only a peculiarity of the technique, because hue biases have also been reported in single-unit data. It is probably most productive to compare the present DG results with results generated previously in the same laboratory, using the same type of stimuli, lighting conditions, and general experimental procedure. In a large sample of striate neurons, Thorell (1980) and Thorell et al. (1984) counted the number of cells responding maximally to the onset of light across different portions of the spectrum. Cells responding maximally to red and blue were the most common type of color cell, and color cells responding most to green and yellow were progressively less common. Thus, the nature of the hue bias in Thorell et al. (1984) appears to be quite similar to that seen in the present DG results. A hue bias has also been reported by Kruger and Gouras (1980), but the bias reported in that study is weaker than that reported here, and different in nature from that seen in this and the Thorell et al. (1984) study.

In fact, results from both the present and the Thorell et al. study may reflect color-opponent processes that are already well understood. The cross-point (that is, the point along the spectrum where a color-opponent cell turns from excitation to in-

hibition) for red–green opponent cells is near 560 nm (e.g., De Valois et al., 1966; Derrington et al., 1984). Since red–green color-opponent cells are the most common variety (and the most consistent with regard to cross-point), it is possible that wavelengths near 560 nm produce little DG uptake because they cause little change in the firing of the predominant type of color-opponent cell. In fact, the dominant wavelengths of the "green" and "yellow" stimuli used in the present study were 552 and 578 nm, respectively; both are reasonably close to the red–green cross-point of ~560 nm. The real problem with this idea is that the lack of DG uptake in response to wavelength variations between 550 and 580 nm appears more total than one might have expected from the behavior of striate single units. However, it may be possible to invoke nonlinearities or thresholds in DG uptake to account for the discrepancy; such nonlinearities can be seen in tests of orientation-specific periodicities in area V2 (R. B. H. Tootell et al., unpublished observations).

Variations with eccentricity

Levels of DG uptake produced by equiluminant color-varying stimuli remain relatively constant with eccentricity across the central 10° or so. (In those few cases in which it does not, the relevant variable is the spatial frequency rather than the spectral composition of the stimulus.) Since the cones mediate color vision, this lack of DG variation with eccentricity is significant, because the density of the cones falls off rapidly away from the fovea. Thus, if one could label color-specific activity with DG at the photoreceptor layer, one would expect a distinct falloff in overall DG uptake away from the fovea. In the striate cortex, one might logically expect the *reverse* of this pattern (that is, a decreased uptake near the fovea), because the striate cortical magnification factor is significantly steeper than the retinal cone separation (Rolls and Cowey, 1970; Perry and Cowey, 1985).

Regardless of the nature of a priori expectations, the fact that color-specific DG uptake is unchanged with eccentricity appears to be a significant departure from a chance result. The result can be interpreted as indicating a neural apportionment of equal amounts of color information to areas of equal striate size. The anatomical results suggesting an equal color sensitivity with eccentricity are in many ways analogous to the psychophysical demonstration that color vision does not decrease with eccentricity if stimuli are correspondingly enlarged at increasing eccentricities (e.g., Abramov and Gordon, 1977; Gordon and Abramov, 1977; Noorlander et al., 1983).

Since the number of cones and the striate cortical magnification are not well matched, the difference might be made up by increasing or decreasing the divergence/convergence of cones feeding into striate cortex. Some part of the difference may be made up at the ganglion cell layer, in which the magnification matches that of striate cortex more closely, though far from exactly (Rolls and Cowey, 1970). Alternatively, the percentage of cones feeding into the color-specific (as opposed to the luminance-specific) channels may change across the retina in parallel with the striate magnification factor; such a difference would not be visible in published cone counts. A third possibility is that the gain of the color-specific inputs varies with eccentricity. Any of these mechanisms would passively produce equal levels of color-specific DG uptake across striate cortex.

Note added in proof: Although the preliminary DG analysis in Figure 8, *A* and *B*, does not support a segregation of hue in different blobs, or in different portions of the same blob, evidence for such an architecture has accumulated from electrophysiological studies (e.g., Ts'o et al., 1986), so we consider this still to be an open question.

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