Spatial Frequency Columns in Primary Visual Cortex

Abstract. *Using the activity-dependent 2-[^{14}C]deoxy-D-glucose technique, we have demonstrated a columnar organization of spatial frequency–specific sensitivity in striate cortex. Cats viewing patterns containing a single spatial frequency presented at all orientations show columns of increased deoxyglucose uptake extending through all cortical layers. A control stimulus containing all spatial frequencies presented at all orientations produces no columnar density differences within the striate cortex.*

A considerable amount of physiological evidence (*1*) has accumulated in recent years about the spatial frequency and orientation specificity of cells in the striate cortex. These cells can be functionally described as spatially localized two-dimensional spatial frequency filters, each cell being sensitive to a more or less limited range of orientations and spatial frequencies of patterns in a given region of the visual field. The ensemble of cells in a region includes all combinations of orientation and spatial frequency and thus all of two-dimensional spatial frequency space. We are concerned here with the anatomical arrangement of the cells tuned to different ranges within the dimensions of spatial frequency and orientation.

The systematic retinotopic mapping of different visual loci onto the surface of the striate cortex has long been established (*2*). Each retinal area projects onto a larger cortical region, the cortical magnification varying inversely with eccentricity (*3*). More recently, Hubel and Wiesel (*4*) have found evidence in single-cell recording experiments for a systematic organization of cortical cells tuned to different orientations of patterns, all receiving information from a given locus in the visual field. All the cells within a cortical column at right angles to the cortical surface have much the same orientation tuning. Neighboring cortical regions vary systematically in their orientation tuning and cover all possible orientations within what Hubel and Wiesel term an orientation "hypercolumn." Groups of orientation hypercolumns appear to be arranged in such a way that columns of cells with similar orientation tuning (but different visual receptive field loci) run along cortex in orientation "slabs" (*5*, *6*) (see Fig. 3A).

Is there an analogous organization of cells tuned to different spatial frequencies, within a cortical region corresponding to a single retinal locus? Based on single-unit experiments, Maffei and Fiorentini (*7*) have proposed a laminar (perpendicular to columnar) organization for spatial frequency. Preliminary single-unit evidence by Thompson and Tolhurst (*8*) indicates that striate cells with similar spatial frequency tuning are found near each other, but in that study the organizational axis was left undefined. In our single-unit experiments, a probe normal to the cortical surface tends to encounter cells with a similar spatial frequency tuning, suggestive of a columnar rather than laminar organization. However, these are difficult questions to settle with single-cell recording procedures.

Here we report a study of striate spatial frequency organization, in which we used the 2-[^{14}C]deoxy-D-glucose (2DG) technique developed by Sokoloff *et al.* (*9*). This technique allows one to see the relative activity of (and anatomical relations among) millions of cells, rather than just a few in one region. Using this technique, Stryker *et al.* (*5*) and Hubel *et al.* (*6*) have obtained striking anatomical confirmation for the orientation columns and arrangement into hypercolumns which they had found in earlier single-cell recording experiments. In the course of various control studies associated with the present experiment, we have repeated their cat orientation experiment (*5*) and confirmed their results. In cats binocularly exposed to a visual stimulus of one orientation, dark autoradiographic columnar patterns are seen at regular intervals across the stimulated region of the striate cortex. In further experiments, we have injected cats with 2DG while they binocularly viewed a control pattern that varied continuously in both orientation and spatial frequency (N = 4) or a blank screen (N = 2). These animals produced autoradiographs without any columnar density differences. Dotlike differences in long-term metabolic activity have been shown in the monkey cortex (*10*) but not in the cat cortex (*11*). Thus the unstimulated cat cortex offers a null baseline condition on which effects of visual stimulation can more readily be assessed.

In all cases to be described, the cats were paralyzed to prevent eye movements and prepared as for single-unit recording (*12*). After accommodation was paralyzed, the eyes were refracted and corrective lenses were used to focus the animal's eyes in the plane of the oscilloscope face, 29 cm away. Binocular convergence in the plane of the stimulus scope was achieved by inserting variable prisms in front of both eyes and adjusting them until the receptive fields of single (or multiple) units recorded from the striate cortex were in register. Stimuli were presented at a mean luminance of 27 cd/m^2 over a circular area 36° in diameter, centered on the area centralis projection. Gratings of 90 percent contrast were drifted across the screen at 1 to 3 Hz, the optimum drift rate for most striate neurons (*13*). When orientation of the stimuli was to be varied, it was changed systematically throughout the 2DG perfusion period, all orientations and all drift directions being presented for the same length of time during each minute. Since the uptake from a single

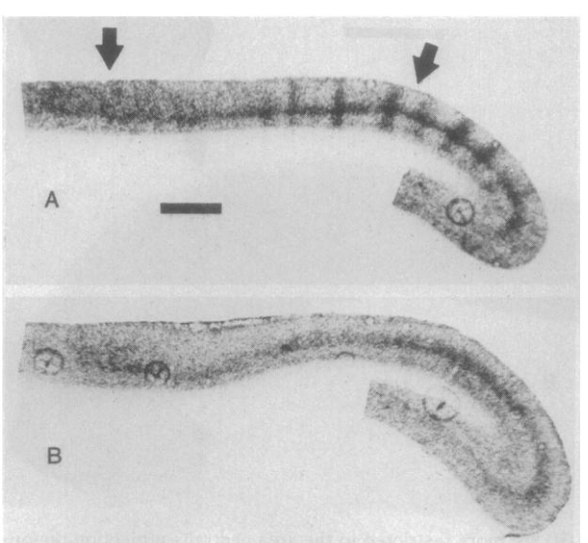

Fig. 1. Comparison of autoradiographs from the striate cortex of two cats. One cat (A) viewed a pattern containing a single spatial frequency (2.0 cycle/deg), and the other (B) a pattern containing multiple spatial frequencies. Both patterns were presented binocularly and at all orientations. Discrete dark columns are seen in the single spatial frequency case (A) but not in the multiple frequency animal (B). In animals that viewed a high-frequency pattern, the columns are restricted to the center of the striate cortex (arrow on right), even though the visual pattern extended in visual space as far as is indicated by the arrow on the left. The autoradiographs are taken from horizontal sections cut at the same depth. Bar is 2 mm.

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pulse of 2DG is nonlinear over time (*9*), the 40 μCi of 2DG per kilogram of body weight was injected continuously over the first 20 minutes to prevent spurious orientation-dependent uptake. The cats were killed with an overdose of barbiturate 45 to 60 minutes after the first injection. They were then quickly perfused (*14*) with a 3.5 percent Formalin and 5 percent sucrose solution, and the brains were removed and frozen in heptane (−50°C). Standard processing procedures followed (*9*), with some modifications. In some cats, the striate cortex was dissected free from the rest of the brain and mounted flat before freezing. The patterns so obtained did not differ from previous sections cut in the conventional manner, except that the expanse across cortex within which these patterns were visible was greatly magnified.

A columnar organization of spatial frequency–specific sensitivity was demonstrated by binocularly presenting cats with a stimulus containing only a single spatial frequency (a sine-wave grating), which was systematically presented at all orientations. Nine animals were studied, each at one of the following spatial frequencies: 0.25 (N = 2), 0.3, 0.5, 0.75, 1.0, 1.8 (N = 2), and 2 cycle/deg. In all nine cases, densely labeled columnar patterns were seen in the striate cortex, perpendicular to and extending across all layers (Fig. 1A). The distance between columns (about 0.8 to 1.0 mm) is similar to, or slightly larger than, that previously reported for ocular dominance and orientation (*5*) columns. Layer 4 labeling was invariably darker than surrounding layers; this increased metabolic activity can be attributed to geniculocortical afferents and possible local first-order striate processing. In no case did we see any lamina-specific density differences which correlated with the spatial frequency of the stimulus; any differences across animals in average laminar density (except layer 4) were minimal. Our results thus indicate a columnar (not a laminar) organization of spatial frequency sensitivity in the striate cortex.

Assuming a columnar spatial frequency organization with columns of slightly different frequency tuning anatomically adjacent to each other, one would expect that a stimulus composed of all spatial frequencies (at all orientations) would excite all cortical cells in a relatively uniform manner. Thus, such a stimulus should produce no columnar autoradiographic differences in the striate cortex. We carried out this control experiment in four cats, using spatial frequencies which varied systematically over the range of 0.25 to 2 cycle/deg. We found no columnar density differences (Fig. 1B).

Further evidence that the columnar organization we observed is actually based on spatial frequency and not due to some confounding variable comes from a comparison of animals tested with high and low spatial frequencies. In high-frequency animals, columns were observed only within 5° of the area centralis projection region, although the stimulus extended 18° peripherally on all sides (Fig. 1A). With low spatial frequencies, the columnar patterns extended across the full 36° stimulus projection region in area 17. These contrasting results can be interpreted as an anatomical confirmation of previous single-unit results in the cat visual cortex (*13*), that cells sensitive to higher spatial frequencies are confined to within about 5° of the area centralis region in area 17, whereas lower frequency units are much more widely distributed.

Although the periodic patterns of increased density in the autoradiographic sections are apparent, it seemed useful to quantitatively examine more subtle aspects of the patterns. We therefore made densitometry measurements on a number of sections with a computer-controlled microdensitometer. Both a periodic increase in density in the spatial frequency columns and a decrease in 2DG uptake between the spatial frequency columns (relative to more peripheral areas in which there were no columns),

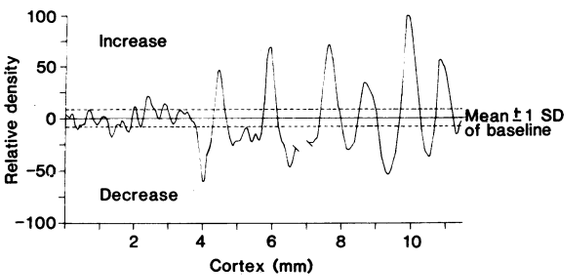

Fig. 2. Densitometry measurements taken from left to right, of layers 1, 2, and 3 of the striate cortex in Fig. 1A (beginning near the arrow on the left). The dark columns in Fig. 1A appear in this graph as precipitous increases in autoradiographic density, and in the intercolumnar regions there is an obvious decrease in density, relative to baseline regions. The small break in the graph is due to a bubble. Measurements were made with a densitometric aperture of 50 × 800 μm and smoothed with a Gaussian filter. Also shown are the mean (± 1 standard deviation) of the baseline.

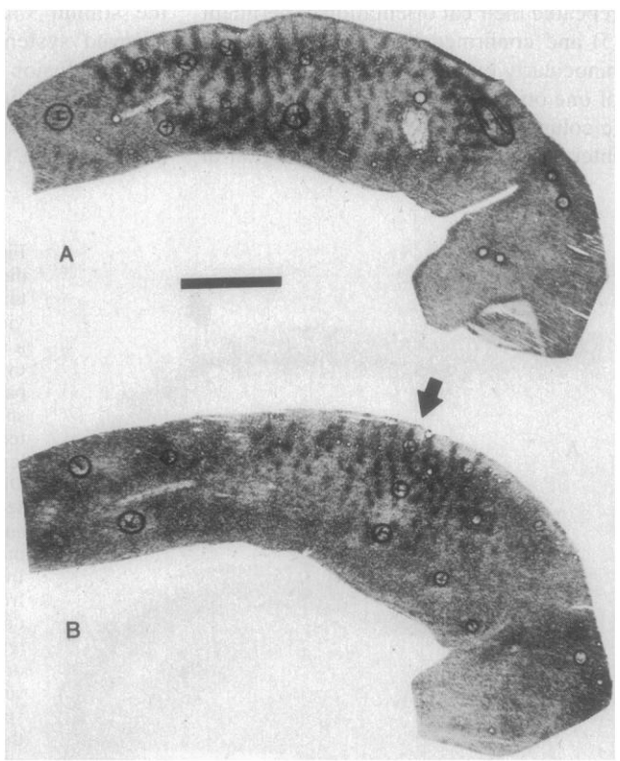

Fig. 3. Orientation slabs in striate cortex in two litter-mate cats. Both cats viewed elongated, horizontally oriented visual patterns, but one (A) viewed a pattern made up of a broad range of spatial frequencies; whereas the other (B) viewed one spatial frequency (1.8 cycle/deg). The plane of section in these autoradiographs is parallel to the cortical surface, so that the viewer is looking at the columns end-on. The full extent of the striate cortex in one hemisphere is visible as a result of a procedure in which the cortical convolutions are unfolded and flat-mounted before sectioning. The horizontal orientation slabs produced by the multiple spatial frequency pattern in (A) are broken apart into relatively discrete horizontal orientation columns when produced by the single frequency pattern in (B). The orientation columns produced with the high spatial frequency stimuli in (B) are more restricted to the area centralis projection region (arrow) than are the multiple frequency slabs in (A). Calibration bar equals 5 mm.

are visible in measurements of layers 1, 2, and 3 (Fig. 2). Although other interpretations are possible, one is that the decrease is due to spatial frequency inhibition, such as has recently been implicated in psychophysical (*15*) and physiological (*16*) studies. That is, the decrement in 2DG uptake between columns may be due to the inhibition (by the cells tuned to the high spatial frequency test pattern) of those cells tuned to lower spatial frequencies in neighboring spatial frequency columns.

Orientation slabs are made up of columns of cells tuned to the same orientation (Fig. 3A), and spatial frequency slabs are made up of columns of cells tuned to the same spatial frequency. How, then, are the orientation and spatial frequency "slabs" related to each other? Preliminary 2DG evidence indicates that these slabs run in somewhat different directions across the cortical surface. Thus the autoradiographic pattern from a cat shown all spatial frequencies at a single orientation has a slablike appearance (Fig. 3A). The autoradiograph from an animal shown a single spatial frequency at a single orientation, however, is more dotlike (Fig. 3B), reflecting the intersections of spatial frequency and orientation slabs. Preliminary accounts of these intersection results have appeared (*17*).

The results indicate that striate neurons tuned to particular spatial frequencies are anatomically arranged in columns, perpendicular to the cortical surface. High spatial frequency columns are confined to the central striate cortex, and low spatial frequency columns extend peripherally, as one would predict from the well-known falloff in acuity with eccentricity. The evidence is compatible with an orderly intersection of spatial frequency and orientation slabs, and a coextensive [and possibly random (*6*)] intersection of ocular dominance slabs. Functionally, this cortical arrangement could form an anatomical substrate for a local, two-dimensional spatial frequency by orientation analysis of information in the visual world.

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Competition Between Ant Species: Outcome Controlled by Parasitic Flies

Abstract. *Experimental evidence demonstrates that the parasitic phorid fly* Apocephalus *shifts the competitive balance between the ant species* Pheidole dentata *and* Solenopsis texana *by interfering with the defensive behavior of* Pheidole dentata *major workers (soldiers). This represents one of the first examples of a parasite affecting competitive interactions among terrestrial animals in natural communities. Similar complex interactions are probably common in many ant communities.*

Although several theoretical (*1*) and laboratory (*2*) investigations suggest that parasites and parasitoids may alter biotic interactions among host species, their role in organizing natural communities has received little experimental study. I now present evidence that the outcome of competition between two species of ants is altered by the presence of a species of fly that is parasitic on one of the ant species. These results are significant in that the effects of higher trophic levels on interactions among terrestrial animals have seldom been investigated in natural communities (*3*), and past studies on interactions among ant species have served as a principal source of documentation for general competition theory (*4*, *5*). Most of the studies have been comparative rather than experimental, and the effects of disturbance, parasitism, and predation have not been investigated. When competition among species involves direct behavioral interactions, as is often the case in ants (*5*), alterations of these interactions arising from the presence of parasites or predators may lead to rapid shifts in community organization.

Wilson (*6*) investigated defense behavior in laboratory colonies of *Pheidole dentata*, a myrmicine ant species found

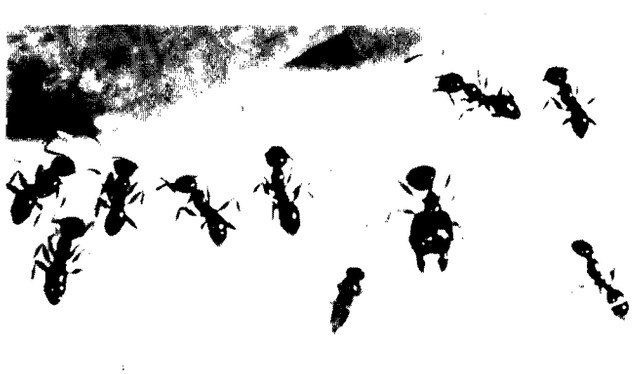

Fig. 1. Parasitic phorid fly, *Apocephalus*, hovering near major worker of the ant *Pheidole dentata*. Within seconds after this photograph was taken, the fly attempted to oviposit on the major worker.

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