The 11th J. A. F. Stevenson Memorial Lecture[1]
Blobs and color vision

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When the monkey striate cortex is stained for the mitochondrial enzyme cytochrome oxidase a polka-dot pattern of patches or blobs is observed in layers 2 and 3 and more faintly in layers 5 and 6. In the macaque these blobs are aligned along the centers of ocular dominance columns. Cells within blobs lack the orientation selectivity and instead have the simpler concentric center-surround fields common in geniculate cells. Blob cells are specifically concerned with color and in particular with maintaining color constancy despite marked changes in the spectral content of the light source.

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Lorsqu'on colore le cytochrome oxydase enzymatique mitochondrial du cortex strié du singe, il se forme un pointillé de plaques ou de taches dans les couches 2 et 3, pointillé qui s'atténue dans les couches 5 et 6. Chez le macaque, ces taches longent les centres des colonnes de dominance oculaire. Les cellules qui se trouvent à l'intérieur des taches sont dépourvues de la sélectivité d'orientation, possédant plutôt les champs concentriques plus simples observés couramment dans les cellules géniculées. Les cellules des taches sont associées spécifiquement à la couleur et en particulier au maintien de la permanence du colorant malgré de nettes variations du contenu spectral de la source lumineuse.

[Traduit par le journal]

Two main topics will thread their way through this lecture: the structure of the monkey striate cortex, including its inputs and outputs, and the physiological basis of color vision. When we began this work in 1980 we did not set out to study color, but the structures in the cortex that we have been looking at turn out to be strongly involved in that sense.

The work to be described was done entirely in macaque monkeys and squirrel monkeys. We have not used monoclonal antibodies, as is so much the fashion today, but our work does touch on immunology in one important way: we got our squirrel monkeys at cut rate from an immunologist because they had stopped producing antibodies!

First let us remind you of the structure and connections of the monkey striate cortex. In the classical visual pathway in mammals, information is transmitted from the eyes to the lateral geniculate body and from there to the primary visual cortex. Each geniculate layer receives its input from one eye only, and a cell in the lateral geniculate is consequently supplied by a single eye, the left or right, depending on the layer in which that cell is situated (Fig. 1). The magnocellular geniculate layers project to layer 4 Cα, the parvocellular to 4 Cβ, with small contributions to 4 A and 6 (Fig. 2). The output of the cortex is from pyramidal cells of the upper layers (2 and 3) and the lowermost layers (5 and 6); layer 4 cells do not project out of the cortex. Layers 2 and 3 send their axons mainly to other cortical regions, and it is these pathways that are presumably involved in perception. Layers 5 and 6 project mainly to subcortical areas, especially to the superior colliculus and, in a recurrent path, back to the lateral geniculate.

When responses were studied at different levels in the path from retina to cortex it was found that up to and including layer 4C, cells responded best to spots of light, and usually had concentric, center-surround receptive fields, whereas most or all cells in the upper layers (2 and 3) and lower layers (5 and 6) responded best to specifically oriented slits, bars, or edges of light (Hubel 1982). Taken literally, this would mean that the entire output of the striate cortex consisted of orientation specific cells, and, in particular, that the entire projection of the upper layers to other cortical regions was in the form of orientation specific cells. As we shall see, these generalizations turn out to require some revision.

For years one has known that cortical cells are functionally segregated in two different ways. A fiber from a single layer of the lateral geniculate body, and hence from one eye, breaks up as it approaches layer 4 of the cortex into patches of terminals with terminal-free gaps between (Ferster and LeVay 1978). All the fibers be-

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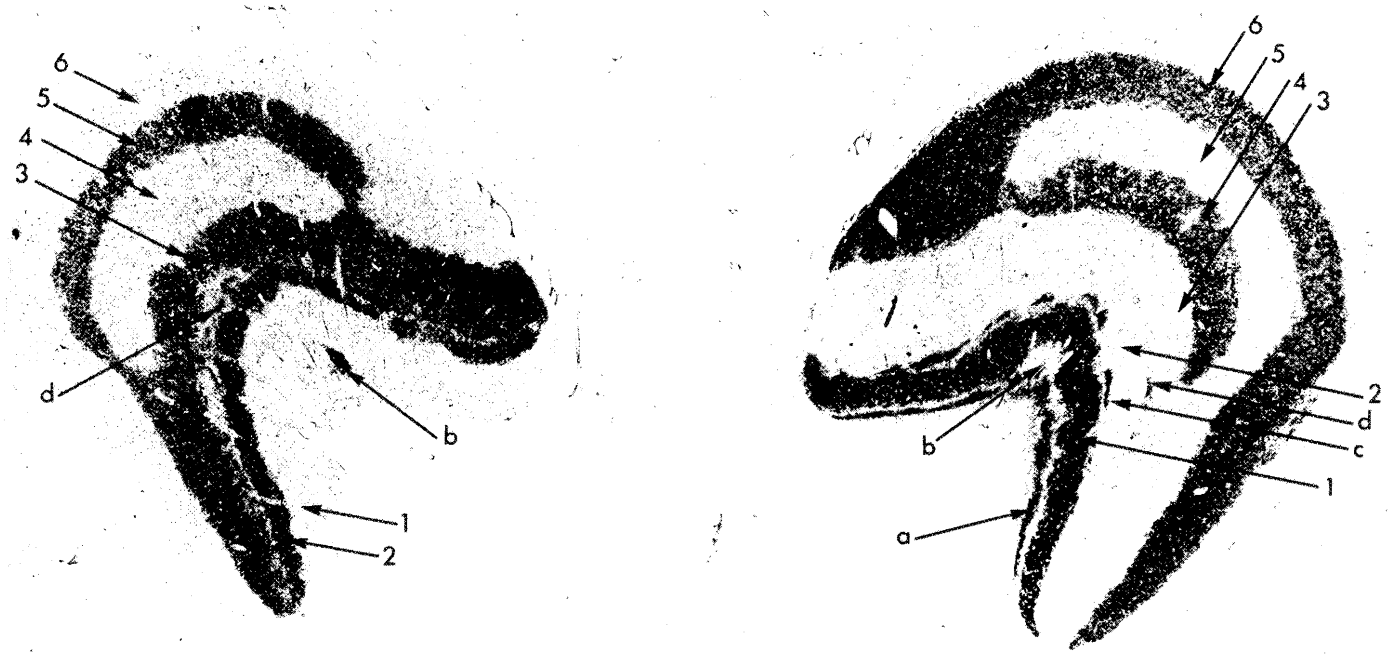

FIG. 1. Autoradiographs of left and right lateral geniculate bodies of a one-week-old monkey whose left eye was injected at birth with tritiated fucose. Light field: labelled regions are black. 1–6 are the classical six layers, numbered from ventral dorsally, and represent four additional regions of input: *a* and *c* are supplied from the contralateral eye, *b* from ipsilateral, and *d* is apparently supplied by both eyes, possibly as alternating band-like monocular regions. (From Hubel and Wiesel (1977), reprinted with permission.)