Retinogeniculate Terminations in Cats: Morphological Differences between X and Y Cell Axons

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sensory" on the basis of both corticocortical connectivity and neuronal responses to more than one modality of sensory information (13) also showed relatively high levels of [3H]naloxone binding. These fields included the superior temporal polysensory cortex (Fig. 2a), the ventral temporal polysensory cortex (14), part of the inferior parietal lobule (15), and the orbital frontal cortex (Fig. 3a) (14). The ventral temporal and orbital frontal fields had among the highest levels of binding in the cortex.

If increased opiate receptor density indicates greater functional importance, then the laminar and areal patterns of opiate receptors shown by the present investigation indicate that opiates are important in the modulation of specific cortical elements. It appears that opiates may predominantly influence the outflow of cortical fields and those fields involved in polymodal information processing and limbic functions.

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References and Notes
7. Although we refer only to opiate receptors in this report, it is recognized that the present binding conditions and ligand were selected to demonstrate the μ opiate receptor (O). The peptide-prefering μ opiate receptor is thought to be distributed relatively homogeneously in the monkey cortex (3).
9. The cerebral cortex can be divided into three strata. These are, in order of increasing depth, the supragranular layers (layers I, II, and III), the internal granular layer (layer IV), and the infragranular layers (layers V and VI).
10. The term "perristriate visual cortex" indicates area OB (16), p. 73.
14. G. von Bonin and P. Bailey, The Neocortex of Macaca mulatta (Univ. of Illinois Press, Urbana, 1947). The ventral temporal polysensory cortex corresponds to their areas TF and TH, while the orbital frontal cortex is the inferior part of area FD.
16. We thank E. V. Evarts, E. G. Jones, M. Mish- kin, W. T. Newton, and W. Stewart for their comments on the manuscript.
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Abstract. We injected horseradish peroxidase into single, physiologically identified, optic tract axons of X and Y cells in cats and studied their termination patterns in the lateral geniculate nucleus. All X cell axons innervate lamina A or AI in narrow zones, and some sparsely innervate the medial interlaminar nucleus. All Y cell axons have broad terminal zones in laminae A and C (from the contralateral retina) or lamina AI (if ipsilateral), and most innervate the medial interlaminar nucleus densely.

The cat's retinogeniculocortical pathways are represented by W, X, and Y cells in the retina and in the lateral geniculate nucleus. These form three parallel, largely independent neural systems that appear to analyze different features of the visual scene (1). We know a great deal about physiological differences among these cell classes but little about morphological differences that underlie the physiology. This is because of the difficulty of directly identifying W,
X, or Y cells for morphological analysis. Such morphological knowledge is essential for our understanding of how these different neural systems are functionally organized. The different morphological features of geniculate W, X, and Y cells in cats have been examined by the technique of intracellular injection of horseradish peroxidase (HRP) into physiologically identified neurons (3). We now describe our use of the same techniques to study the functional organization and morphology of X and Y cell retinogeniculate terminals. We found a number of morphological differences between these two physiological pathways, and these differences are important to the way retinal X and Y cells transmit visual information centrally.

Our general experimental methods have been described (2, 4). Optic tract axons were recorded first extracellularly within or ventral to the lateral geniculate nucleus (see Figs. 1, A and B, and 2, A and B), and they were identified as X cell or Y cell by standard criteria (5). They were then impaled. Identification was verified intracellularly, and then HRP was injected into the axon by iontophoresis with depolarizing pulses of up to 20 nA at 4 to 8 Hz for several minutes. After a 2- to 20-hour survival for each injected axon, the cat was killed for histological examination.

We have thus obtained structure-function correlations for 16 X cell and 12 Y cell axons. In this report, we describe the appearance of terminal zones within the main geniculate laminae (that is, the A and C laminae (6)). The morphology correlates well with the X cell or Y cell physiological classification, but we found no obvious morphological correlate to ON and OFF center responses. Figure 1, B to D, shows the morphology of a typical X cell terminal zone, and Fig. 2, B to D, does likewise for a typical Y cell terminal zone. Our data for Y cells confirm and extend those of Bowling and Michael (7). Five major morphological differences can be described between retinogeniculate X cell and Y cell axons. These include differences in axon diameter, axon location within the optic tract, regions of termination, geometry of terminal fields, and the structure and arrangement of individual boutons.

1) Within the optic tract, X cell axons are thinner than Y cell axons. We measured axon diameters to the nearest 0.5 μm (2). The mean diameter for 13 X cell axons that we could trace through the optic tract was 2 μm, and the range was 1.5 to 2.5 μm. The corresponding values for the 12 Y cells were 3 μm and 2 to 4 μm. Within the lateral geniculate nucleus, however, X cell and Y cell axons branch repeatedly before terminating. Since the preterminal branches of X cell and Y cell axons are equally fine, fiber diameter within the lateral geniculate nucleus should not be used to infer cell type.

2) Within the optic tract, X cell axons tend to lie dorsal to Y cell axons, with little or no overlap. All of the 13 X cell axons lie in the dorsal third of the optic tract. All of the 12 Y cell axons lie ventral to the X cell axons. These observations are consistent with prior reports that thicker axons are more ventrally located than thinner ones in the optic tract (8).

3) Y cell axons have more extensive and more widely branching terminal fields than do X cell axons. Every X and Y cell axon in our material exhibits a terminal zone in lamina A or A1, although terminal zones elsewhere are more variable (see below). From the contralateral retina, Y cell axons branch extensively to provide large terminal fields in laminae A and C and in the superior colliculus. Those from the ipsilateral retina branch to innervate lamina A1 and the superior colliculus. Most of the Y cell axons also densely innervate the medial interlaminar nucleus (a subdivision of the lateral geniculate nucleus), but a minority (5 of 12 in our sample) do not (Fig. 2B). In the earlier description (7), each of the nine recovered Y cells innervated the medial interlaminar nucleus. To date, we have not seen obvious physiological differences between Y cells that innervate the medial interlaminar nucleus and those that do not, nor do these groups of Y cells obviously differ with regard to their terminal zones within the A laminae. In contrast to the Y cell terminal zones, those of X cells lie only in lamina A or A1. However, 2 of the 12 X cell axons from the contralateral eye branch to yield a few terminals in lamina C. Eleven X cell axons continue posteriorly into the brachium of the superior colliculus (Fig. 1B). Of these, four issue sparse terminals into the medial interlaminar nucleus.

4) Perhaps the clearest difference between X cell and Y cell terminal zones lies in their geometry within the A laminae (see Figs. 1 and 2). The terminal zones of X cells are small and typically cylindrical, with the long axis perpendicular to the geniculate laminae. Y cell terminal zones are more variable in

Fig. 2. Data from a Y cell axon driven by the right eye (contralateral to the recording site). Most conventions are as in Fig. 1. The axon's receptive field had an OFF center of 1.2° diameter located 11.5° from the vertical meridian and 3.5° below the horizontal zero parallel of the visual field. The conduction latency from the optic chiasm to the recording and injection site [open arrow in (B)] was 0.5 msec. (A) Intracellular recording. The bar below part of the trace indicates the presence of a small black spot placed in the receptive field center. Note the transient response to this stimulus. (B) Drawing of the left lateral geniculate nucleus and axon from 27 consecutive, 100-μm-thick coronal sections. The parent trunk of the axon is 4 μm thick, and the medial branch passes posteriorly beyond the medial interlaminar nucleus (MIN), with no terminals there. Geniculate terminals are limited to laminae A and C. (C) More detailed drawing of the terminal zones in laminae A and C. (D) Location and shape of the 1405 terminal boutons in lamina A, reconstructed from six consecutive, 100-μm-thick coronal sections. (E) Morphology of typical terminal bouton arrangements in lamina A. Note both the lack of bouton clustering and their relatively heterogeneous composition (see text and compare with Fig. 1E).
The X and Y cell pathways show that these indeed represent distinctly different neural circuits.

References and Notes
4. The cats were anesthetized, paralyzed, artificially ventilated, and optically refocused. Fine micropipettes filled with 3 percent HRP plus 0.2 M KCl and 0.05 M Tris and beveled to an impendence of 90 to 150 megohms at 100 Hz were used to record activity from geniculate neurons and optic tract fibers. These microelectrodes were placed through a hydraulically sealed cranialotomy and durotomy. Bipolar stimulating electrodes were placed across the optic chiasm to stimulate optic tract fibers. After the physiologic data collection and HRP injections, the cats were given large doses of barbital and perfused transcardially with saline and fixative. The brains were then removed, cut coronally at 100 μm, and reacted with 3,3′-diaminobenzidine. The reaction product was intensified by treatment with cobalt chloride. Further details can be found in (2).
5. X- and Y-cell axons were distinguished by the following criteria (see K.-P. Hoffmann, J. Stone, S. M. Sherman, J. Neurophysiol. 35, 518 (1972); S. Hochstein and F. M. Shapley, J. Physiol. (London) 262, 237 (1976); M. H. Rowe and J. Stone, Brain Behav. Evol. 14, 185 (1977); S. Lehmkuhle, K. E. Kratz, S. C. Mangel, S. M. Sherman, J. Neurophysiol. 43, 420 (1980). X cells respond linearly to counterphased, sine-wave gratings, whereas Y cells respond nonlinearly; X cell axons respond to the onset of opto-chiasm stimulation than do Y cell axons (mean and range for X cells, 0.8 msec and 0.7 to 1.0 msec; for Y cells, 0.4 to 0.7 msec). X cells tend to have smaller receptive field centers than do Y cells; X cells respond to faster moving targets than do those of Y cells.

Hemispheric Asymmetries in the Behavioral and Hormonal Effects of Sexually Differentiating Mammalian Brain

Abstract. Estrogen pellets were placed in either the right or left hypothalamus of newborn female rats so that only one side of this brain area was exposed to the postnatal masculinizing and demasculinizing effects of the hormone. The effects of estrogen on gonadotropin secretion and reproductive behavior depended on both the region and the side of implantation. Exposure of the left hypothalamus to estrogen resulted in demasculinized development. Exposure of the right hypothalamus to estrogen resulted in masculinized development. Thus the response of the developing hypothalamus to gonadal steroids may be asymmetric.

During a restricted period of perinatal development, gonadal steroids act on the mammalian hypothalamus to masculinize or feminize reproductive functions, including behavior (1). Masculinization increases male sexual behavior in adult males or females exposed to testosterone or its metabolite, estradiol (E2); feminization decreases female sexual behavior and eliminates positive-feedback effects on the secretion of luteinizing hormone (LH) in adults exposed to E2. These two aspects of sexual differentiation are independent processes involving separate regions of the hypothalamus (2). We suggest here that the hypothalamus develops asymmetrically with respect to sexual differentiation. When we exposed only the left side of the hypothalamus of neonatal rats to gonadal steroids, development was feminized. When we exposed only the right side of the hypothalamus to gonadal steroids, development was masculinized. Between 24 and 48 hours after birth, 91 female rat pups received bilateral intra-hippocampic implants of steroid (3). Thirty control pups received implants of cholesterol. Experimental females received E2 on one side (31 right, 30 left) and cholesterol on the other. We used E2 as the hormonal stimulus for sexual differentiation because it is the active metabolite of testosterone for this process.