X- and Y-cells in the dorsal lateral geniculate nucleus of the tree shrew (*Tupaia glis*)

S. MURRAY SHERMAN, T. T. NORTON AND V. A. CASAGRANDE

Department of Physiology, University of Virginia, Charlottesville, Va. 22901, Department of Psychology, Duke University, Durham, N.C. 27706, and Department of Anatomy, University of Wisconsin, Madison, Wisc. 53706 (U.S.A.)

Beginning with the work of Enroth-Cugell and Robson[5] in 1966, many investigators have provided evidence that the cat's retino-geniculo-cortical pathway is comprised of two parallel and functionally distinct systems[3,6,10,11,19]. The X-system includes retinal X-cells which project to X-cells in the lateral geniculate nucleus, and likewise, the Y-system includes retinal and geniculate Y-cells. Recently, Stone and coworkers[10,11,18,19] suggested that the X-system terminates upon cortical simple cells and the Y-system upon cortical complex cells.

Despite the extensive data for the cat, no direct evidence for the existence of X- and Y-systems has, to our knowledge, been published for any other mammalian species (however, see ref. 7). In order to test the generality of this concept of parallel processing in mammalian visual systems, we studied the electrophysiological properties of lateral geniculate neurons from tree shrews. These animals have well-developed visual systems and undoubtedly represent quite a different evolutionary history from that of the cat[4,9,14]. We conclude that tree shrews, too, have parallel and distinct X- and Y-systems.

In the cat, differences in electrophysiological properties between X- and Y-cells are quite clear, both in the retina and lateral geniculate nucleus. For example, Y-cells, when compared to X-cells, generally (1) have faster-conducting axons, (2) have larger receptive field centers, (3) respond more transiently to visual stimuli of standing contrast, (4) respond to visual stimuli moving at faster rates, and (5) summate visual stimuli across their receptive fields in a less linear fashion.

We used techniques essentially identical to those employed in cats[11] to test these properties in dorsal lateral geniculate neurons from 8 tree shrews. These were surgically prepared under halothane anesthesia and maintained with N_2O-O_2 (70:30) plus a continuous intravenous infusion of immobilizing agents following an initial 10 mg dose of gallamine triethiodide. The preparation differed from that used for cats[11] only in the following ways. First, we cannulated the bladder, since in early experiments animals died apparently from a failure to expel urine. Second, we found that higher levels of paralyzing agents (gallamine triethiodide, 14 mg/kg/h; D-tubocurarine

chloride, 1.5 mg/kg/h, in dextrose to achieve infusion of 0.24 ml/h total fluid) were needed to control eye movements. Finally, the animals were ventilated at 65–75 breaths/min, 3.1 ml/breath, to achieve an end-tidal CO_2 level of 2.0% (this was continuously monitored).

For placement of our recording and stimulating electrodes, we used appropriate stereotaxic guides[13,20]. Extracellular, tungsten microelectrodes (15–30 MΩ at 60 Hz) were placed into the lateral geniculate nucleus via both horizontal (from the lateral surface) and vertical approaches. Bipolar stimulating electrodes were lowered into the optic chiasm, and an array of 5 electrodes was placed into the striate cortex to allow various combinations of bipolar cortical stimulation. Geniculate neurons were thus activated both ortho- and antidromically, and we used conventional criteria for identifying the results of such stimulation (i.e., see refs. 1, 11).

The animals' corneas were covered with contact lenses of a curvature (3.35–3.40 mm) selected by retinoscopy to make the frontal tangent screen conjugate with the retinal receptor layer. Because retinoscopy generally refracts the eye with respect to the vitreal-retinal surface (cf. ref. 8), we corrected our retinoscopic readings by creating approximately 4D of apparent hypermetropia in the animals. We verified this correction in one tree shrew before fitting contact lenses (i.e., its eyes appeared with retinoscopy to be about 4D hypermetropic).

Visual stimuli consisted of hand-held black or white targets on a gray background; we did not systematically vary stimulus color. We used previously described methods[11] to study the following receptive field properties: (1) the dominant eye for activating the neuron; (2) the presence of concentric center/surround receptive field organization; (3) the size of the receptive field center; (4) the duration for which the cell responded above spontaneous levels while a stimulus of appropriate contrast (i.e., white for ON center, black for OFF center) was held in the field center; (5) the response to moving, square-wave gratings of various sizes (0.55 cycles/degree to 6.66 cycles/degree); and (6) whether or not the neuron was excited by rapidly moving (> 100°/sec) large targets of appropriate contrast to excite the cell through the surround (i.e., black for ON center; white for OFF center).

Receptive fields. Of the 59 neurons studied, 52 had concentric, generally circular, center/surround organization in their receptive fields. Each of these 52 was driven by stimulation of only one eye (41 contralateral, 11 ipsilateral); 14 were ON center, and 38 were OFF center. For reasons given below, these 52 we considered to be geniculate relay cells. None of the remaining 7 neurons could be antidromically activated from the cortex, and they are not considered further here.

We found that, as in the cat, nearly all of these 52 neurons could be placed into one of two groups on the basis of their receptive field properties. Thus, we classified 27 X-cells and 22 Y-cells. We found 3 cells with mixed properties such that neither classification seemed appropriate. Although the receptive field tests that we used displayed slight overlap between X- and Y-cells (cf. refs. 3, 11; see also Figs. 1–3), a given cell had either no (31/49) or one (18/49) receptive field property which failed to correlate with the others in the X/Y classification.

In general terms, therefore, receptive fields of cells in the tree shrew lateral
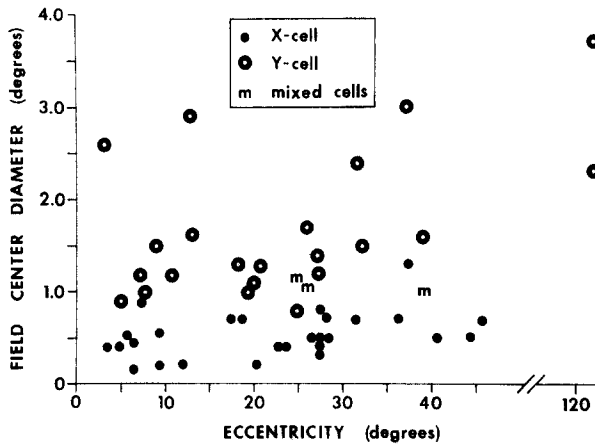
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Fig. 1. Receptive field size as a function of position in the visual field. The 27 X-cells, 22 Y-cells, and 3 cells with mixed properties ('mixed cells') are shown as indicated. Distances from the area centralis are shown on the horizontal axis, and diameters of receptive field centers, on the vertical axis. We used the method of Sanderson and Sherman[17] to estimate as 40° the horizontal separation between the optic disc and area centralis, and we assumed the vertical separation to be 0°. (While these estimates are subject to considerable error for the absolute values on the horizontal axis, the relative field locations are more accurately represented since they were all plotted relative to the optic disc position. Thus, any trends of field size with eccentricity would not be obscured by this error in estimating the area centralis position.) On average, Y-cells had significantly larger field centers than X-cells ($P <$ 0.001 on a t-test). Y-cells averaged 1.7 $\pm$ 0.8, and X-cells, 0.5 $\pm$ 0.2 (mean $\pm$ S.D.). Field center diameter did not correlate with eccentricity for all cells or for the subpopulation of X-cells, but a significant correlation was seen for Y-cells ($r = +0.56$, $P < 0.01$). Thus, X-cells maintained small field centers throughout the visual field whereas centers of Y-cells become progressively larger with eccentricity.

geniculate nucleus displayed the following differences from those of Y-cells. (1) X-cells had smaller receptive field centers than did Y-cells throughout the visual field. This is indicated by Fig. 1 which charts the diameter of the field center as a function of eccentricity in the visual field for each of the 52 neurons. Interestingly, field centers for Y-cells tended to increase with increasing eccentricity, while for X-cells they remained constant (see legend for Fig. 1). This may result from different aspects of the stimulus which are coded by cells of the X- and Y-systems. Fig. 1 also shows no obvious shift with eccentricity in the relative proportion of X- and Y-cells, although sampling errors could obscure such a tendency since we generally recorded X- or Y-cells in groups. In the cat[11], both X- and Y-cells tended to have larger field centers with increasing eccentricity; also, Y-cells became relatively more numerous with increasing eccentricity. (2) X-cells responded tonically to stimuli of appropriate standing contrast (i.e., for more than 30 sec above spontaneous levels), whereas Y-cells responded phasically (i.e., they typically returned to spontaneous levels within 5 sec.) (3) X-cells were generally unresponsive to rapid movements of large discs through the field, and this was particularly apparent when the disc was of appropriate contrast for the surround (i.e., black for ON center fields and white for OFF center fields). Y-cells responded briskly to all such rapidly moving discs. (4) Finally, X-cells as a group responded to
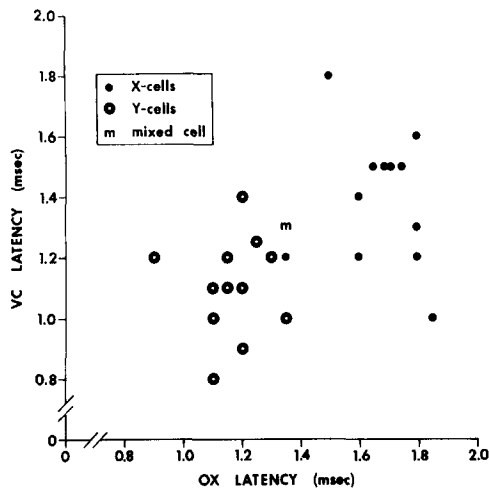
Fig. 2. Relationship between orthodromic optic chiasm (OX) latency and antidromic visual cortex (VC) latency for 25 neurons of the lateral geniculate nucleus. Symbols are identical to those in Fig. 1. While neither X- nor Y-cells as a group displayed a correlation between OX and VC latencies, such a correlation was seen for the entire cell population ($r = +0.51, P < 0.01$). Thus, in general, geniculate neurons with the slower retinal afferents have the slower axons in the optic radiation, and *vice versa*. Y-cells have significantly shorter latencies than do X-cells for both OX and VC stimulation ($P < 0.001$ and $P < 0.01$, respectively, on t-tests). The average values are (mean $\pm$ S.D.): for OX latencies, Y-cells $= 1.2 \pm 0.1$ msec and X-cells $= 1.7 \pm 0.2$ msec; for VC latencies, Y-cells $= 1.1 \pm 0.2$ msec and X-cells $= 1.4 \pm 0.2$ msec.

finer gratings than did Y-cells. Of the 23 X-cells carefully tested in this fashion, 11 responded to gratings finer than 1.2 cycles/degree, while only 1 of 18 Y-cells did so. This was a center response since the surround was masked (the gratings were moved behind a gray card with an aperture which exposed only the field center to the grating). X-cells responded to gratings only by firing in synchrony as each bar passed through the field center. Y-cells, on the other hand, responded either to each bar in synchrony, or non-linearly to movement of the grating — this latter response in Y-cells was usually the only response elicited from the finest grating to which the cell fired.

Electrical activation. Again, as in the cat, we found that axons of tree shrew X-cells conducted less rapidly than those of Y-cells (see Figs. 2 and 3). On average, with an allowance of 0.75 msec synaptic delay and a measured retino-geniculate conduction distance of 6.5 mm from the optic chiasm, the retinal axons terminating on geniculate X-cells conducted at 4–11 m/sec and those terminating on geniculate Y-cells conducted at 9–43 m/sec. For single geniculate neurons, Fig. 2 shows the relationship between latencies of discharge to optic chiasm stimulation (orthodromic) and visual cortex stimulation (antidromic). When compared to the geniculate Y-cells, X-cells both receive from slower conducting retinal axons and have more slowly conducting axons to cortex (see legend for Fig. 2). Therefore, we tentatively conclude that in the tree shrew, as in the cat[3,11], retinal X-cells project to geniculate X-cells and Y-cells to Y-cells.

The 25 neurons shown in Fig. 2 represent confirmed relay cells, since they were
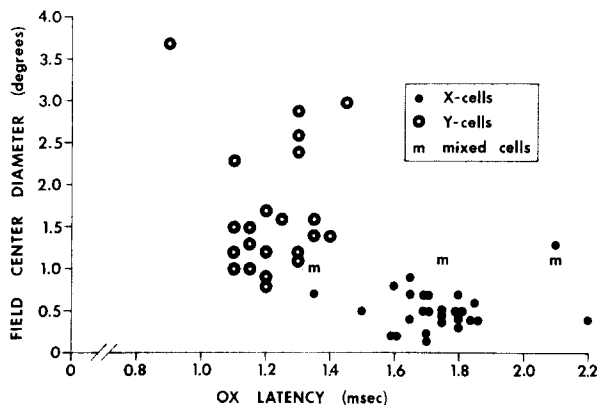
Fig. 3. Relationship between latency to optic chiasm stimulation (OX latency) and receptive field center diameters for the 52 geniculate neurons. Symbols are identical to those in Fig. 1. While neither X-nor Y-cells as a group displayed a correlation between OX latency and field center size, such a correlation was seen for the entire cell population ($r = -0.59$, $P < 0.001$). Thus, in general, cells with the shorter OX latencies have the larger field centers, and vice versa.

antidromically activated from cortex. Since their remaining properties were qualitatively identical to those of the 27 cells not antidromically driven from cortical stimulation, we assume all 52 neurons were relay cells of the lateral geniculate nucleus. The failure to activate over half the cells from cortex is not surprising. For one example, many geniculate neurons presumably project to areas of striate cortex distant from our implanted stimulating electrodes.

Correlations between receptive field properties and electrical stimulation. Implicit in the above discussion is the finding that cells with long response latencies to stimulation of optic chiasm or visual cortex have receptive field properties typical of X-cells, and *vice versa* for Y-cells. One example of this is shown in Fig. 3 which illustrates for single neurons the relationship between the response latency to optic chiasm stimulation and the diameter of the receptive field center. Clearly, neurons with the longer latencies to optic chiasm stimulation have the smallest field centers (X-cells), and those with the shorter latencies, the larger centers (Y-cells).

Conclusions. While undoubted quantitative differences exist between cat and tree shrew geniculate neuronal response properties, the qualitative and fundamental similarity between cat and tree shrew in this respect is impressive. In both species, lateral geniculate relay cells have concentric, ON or OFF center, monocularly activated receptive fields. These can be divided in both animals into X- and Y-cell subgroups, each of which appears to be part of two functional subsystems in the retino-geniculo-cortical pathway. Despite these similarities, cats and tree shrews are not closely related in evolutionary terms, and obvious differences exist in their visual systems. For two examples, cats have predominantly rod retinae[2,12], whereas tree shrews have mostly cones[15], and in the cat the laminated portion of the dorsal lateral geniculate nucleus projects to both areas 17 and 18 (see ref. 16), whereas in the tree shrew, it projects only to area 17 (see refs. 4, 9). That such different animals have X- and Y-cells in common suggests that other mammalian retino-geniculo-cortical pathways may share X- and

Y-subsystems as a general organizational principal. Certainly, X- and Y-cells are not unique to the cat.

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