Vision Res. Vol. 18, pp. 489 to 492

0042-6989/78/0401-0489 $02.00/0

RESEARCH NOTE

ELECTROPHYSIOLOGICAL CLASSIFICATION OF X- AND Y-CELLS IN THE CAT'S LATERAL GENICULATE NUCLEUS

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(*Received* 8 *March* 1977; *in revised form* 22 *June* 1977)

Two classes of cat retinal ganglion cells—X- and Y-cells—have been described by Enroth-Cugell and Robson (1966). X-cells linearly sum the effects of stimuli presented to different parts of the receptive field, whereas Y-cells do not. For example, a "null position" can be found within the receptive field of an X-cell such that an appropriately positioned counterphased grating or bipartite field evokes no response from the cell. Y-cells do not show a null position for such stimuli (i.e. all stimulus positions within the receptive field evoke responses), and therefore these cells do not respond in a linear fashion. Shapley and Hochstein (1975) have extended this linear/nonlinear distinction to X- and Y-cells of the dorsal lateral geniculate nucleus in cats.

Hoffmann, Stone and Sherman (1972) have also classified cat lateral geniculate neurons as X- or Y-cells with a battery of tests which does not include the above-mentioned test for linear vs nonlinear summation (see also Cleland, Dubin and Levick, 1971). In this classification scheme: (1) X-cells have longer response latencies to optic chiasm stimulation than do Y-cells; (2) X-cells are not excited by fast movements of a large target having a contrast opposite to that required to excite the cell through its field center (i.e. a bright target for an off-center cell and a dark target for an on-center cell), whereas Y-cells respond vigorously to such stimuli; (3) X-cells generally respond to higher spatial frequencies of square-wave gratings than do Y-cells, and X-cell responses are always modulated by the grating bars whereas Y-cells typically display unmodulated responses for higher frequency gratings; and (4) X-cells generally give a more sustained response to an appropriate standing contrast stimulus than do Y-cells.

The extent to which the classification scheme of Hoffmann *et al.* (1972) correlates with the linear vs. nonlinear summation criteria of Enroth-Cugell and Robson (1966) has not been directly determined. In the present paper we report the results of studying cat lateral geniculate neurons, both with a battery of tests similar to that used by Hoffmann *et al.* and also with a test for their spatial summation properties by a technique first described by Enroth-Cugell and Robson (1966, p. 538).

We used standard, single-unit extracellular recording techniques to study 75 cells in laminae A and A_1 of the dorsal lateral geniculate nucleus in 9 normal cats. Varnish-insulated tungsten microelectrodes (15–30 MΩ at 500 Hz) were used to record single-unit extracellular potentials. During the recording session, animals were anesthetized with a 70% N_2O–30% O_2 mixture and paralyzed with a continuous infusion of 19 mg/hr Flaxedil in lactated Ringers with 5% dextrose. Animals were artificially ventilated, and their end-tidal CO_2 maintained at 4.0%. The pupils were dilated with atropine sulfate, the nictitating membranes retracted with Neosynephrine, and the corneas protected with zero power contact lenses. Spectacle lenses, if needed, were chosen by retinoscopy to make the retinae conjugate with a frontal tangent screen placed 114 cm from the eyes. Varnish-insulated tungsten electrodes were placed stereotaxically on either side of the optic chiasm for bipolar stimulation of retinogeniculate axons. Latency to optic chiasm stimulation for the lateral geniculate neurons was measured from the stimulus artifact to the foot of the action potential.

Receptive field centers were located using small spots of light produced with a hand projector. All cells tested had their receptive fields within the binocularly viewed portion of the visual field (i.e. 0–45°), and 55 (73%) of the units had their receptive fields within 20° of the area centralis. In addition to measuring latency to optic chiasm stimulation, we used two additional tests utilized by Hoffmann *et al.* (1972). First, a cell's response to the fast movement (200–300°/sec) of a large target was determined by listening to an audio representation of the cell's action potentials. Targets were much larger than the receptive field center and extended well into the surround. For on-center cells a black disc (0.27 cd/m^2 on an ambient background of 6.8 cd/m^2) was used, and for off-center cells a light spot (2.0 cd/m^2 above an ambient background of 0.5–1.5 cd/m^2) was used. Second, a tonic vs phasic response was determined by introducing a target smaller than the receptive field center and timing the duration of the elicited response. Light spots were used for on-center cells, and black discs were used for off-center cells. Cells responding for less than 5 sec were considered phasic, and cells responding for at least 15 sec were considered tonic.

Spatial summation of these same cells was tested by using a 9° × 9° bipartite field. Illumination of the two halves of the stimulus was sinusoidally counterphased by passing a beam of light first through two polarizing filters placed side-by-side with the axes of

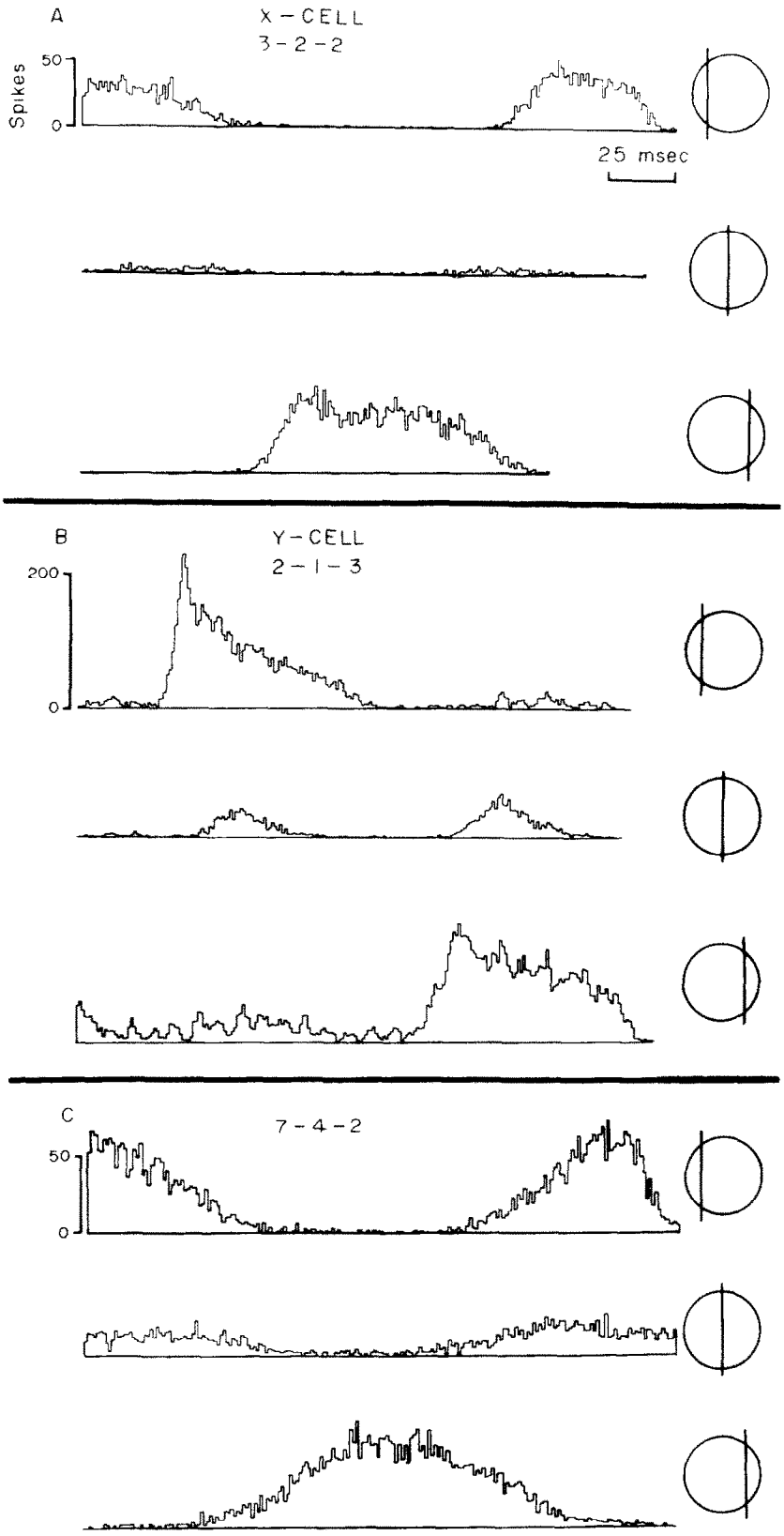

Fig. 1. Response (post-stimulus time histograms) of an X-cell (A), a Y-cell (B), and a cell that could not be classified on the basis of the spatial summation test (C) to 1000 cycles of the contrast reversal stimulus. Receptive field positions for the center of the bipartite field are indicated to the right of the histograms. Note in C that, although for the center stimulus position there is clearly a diminished response in relation to other stimulus positions, no true null exists since a slight modulation is present at this position.

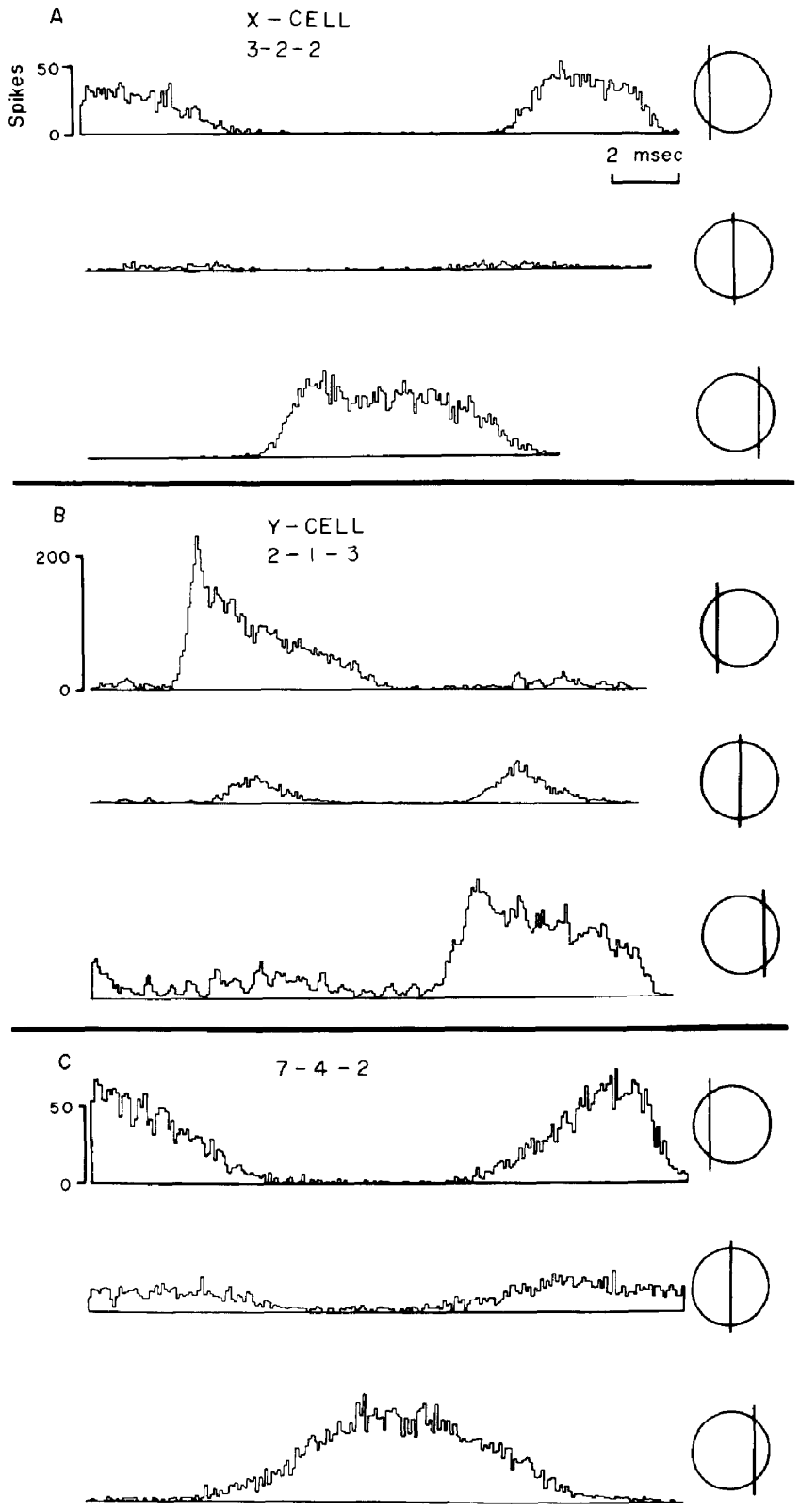

Fig. 2. Latency-frequency histogram as a function of latency to optic chiasm (OX) stimulation. Only those cells for which quantitative data relating firing rate to position of the contrast reversal stimulus are plotted. Note that light bars indicate cells classified as Y-cells and dark bars indicate cells classified as X-cells under the scheme of Hoffmann *et al.* (1972). The cells without hatching were also classified as X or Y on the basis of their spatial summation property (Enroth-Cugell and Robson, 1966), i.e. a null point could be found for X-cells and they were therefore considered linear in their spatial summation. The hatched cells, although classified as X or Y under the scheme of Hoffmann *et al.* (1972) could not be classified solely on the basis of the spatial summation test.

polarization orthogonal to each other, then through another polarizing filter that was rotated at various speeds, with 2.5 rev/sec being the most common. The illumination of the brightest portions of the stimulus field was typically 1.5–2.0 cd/m^2 above an ambient background of 0.5–1.5 cd/m^2. For some cells ambient illumination and stimulus intensity were varied to achieve the maximal response from the cell. The center of the bipartite field was placed at various positions across the receptive field in an attempt to locate a stimulus null position (i.e. where the cell would not respond to the counterphased stimulus). A computer was used to generate histograms relating neuronal discharge to this stimulus for 46 of the 75 cells tested.

As shown in Fig. 1, our results for the spatial summation tests are in agreement with previously reported data (Enroth-Cugell and Robson, 1966; Shapley and Hochstein, 1975; DeMonasterio, Gouras and Tolhurst, 1976). The stimulus produced modulation of the cell's response throughout the receptive field of Y-cells (Fig. 1B), while a null position was evident in X-cells (Fig. 1A). Nearly all of the geniculate cells tested could be easily classified as X- or Y-cells on the basis of the spatial summation test (Fig. 2). A small percentage (roughly 15%), however, could not be confidently placed into one of these two categories (Fig. 2). An example for such a cell is shown in Fig. 1C. Here, a stimulus position was present which, while evoking a rather diminished response, produced a slight modulation in the cell's activity.

Three interpretations of these cells are possible. First, they could be Y-cells with only a minimal response at one position within the receptive field. Second, they could be unusual X-cells having no true null position for the stimulus—only a position that produces a slight, residual modulation at the fundamental frequency of response. Or third, these cells could be typical X-cells, with the residual modulation resulting from some artifact or uncontrolled variable. For instance, since some lateral geniculate cells have extremely small receptive fields, small uncontrolled eye movements could easily lead to such modulations by moving the stimulus intermittently out of the null position. Furthermore, Hamasaki and Sutija (1976) report that the nature of an X-cell's response at the null position can be altered by varying stimulus contrast, stimulus size, or adaptation level.

We found it impossible using this test in a qualitative fashion to differentiate between the above-mentioned alternatives. This type of test therefore is not a definitive test for separating cat lateral geniculate cells since it does not dichotomize all cells as X or Y when used in this manner. Perhaps strict control of above-mentioned potential artifacts and variables, or even the use of a quantitative measure of spatial summation similar to that used by Hochstein and Shapley (1976) for cat retinal ganglion cells, would provide dichotomization. Such a determination, however, is not the point of the present study.

As indicated in Fig. 2, all of the cells could be classified as X or Y on the basis of a battery of tests similar to that used by Hoffmann *et al.* (1972). All of the Y-cells had shorter latencies, all responded vigorously to the fast moving target, and all but 5 gave a predictable phasic response to the standing contrast. Using this battery of tests, even those cells unclassified on the basis of the spatial summation test were classified as X- or Y-cells. The results from those cells not shown in Fig. 2 (i.e. the 29 for which histograms were not collected) agree completely with those shown in Fig. 2. Consequently, as demonstrated with the present sample of cells (Fig. 2), X-cells are X-cells and Y-cells are Y-cells under both the classiffication scheme of Hoffmann *et al.* (1972) and the linear vs non-linear summation criteria of Enroth-Cugell and Robson (1966).

Acknowledgements—This work was supported by USPHS Grant EY 01565. K.E.K. was supported by USPHS Individual Postdoctoral Fellowship EY 05077. S.M.S. was supported by USPHS Research Career Development Award EY 00020.

REFERENCES

Cleland B. G., Dubin M. S. and Levick W. R. (1971) Sustained and transient neurones in the cat's retina and lateral geniculate nucleus. *J. Physiol., Lond.*, **217**, 473–496.

De Monasterio F. M., Gouras P. and Tolhurst D. J. (1976) Spatial summation, response pattern, and conduction velocity of ganglion cells of the rhesus monkey retina. *Vision Res.* **16**, 674–678.

Enroth-Cugell C. and Robson J. G. (1966) The contrast sensitivity of retinal ganglion cells of the cat. *J. Physiol., Lond.* **187**, 517–552.

Hamasaki D. T. and Sutija V. G. (1976) Sustained search for linear Y-cells. *Neurosci. Abs.* **2**, 1603.

Hochstein S. and Shapley R. M. (1976) Quantitative analysis of retinal ganglion cell classifications. *J. Physiol., Lond.* **262**, 237–264.

Hoffmann K.-P., Stone J. and Sherman S. M. (1972) Relay of receptive field properties in dorsal lateral geniculate nucleus of the cat. *J. Neurophysiol.* **35**, 518–531.

Shapley R. and Hochstein S. (1975) Visual spatial summation in two classes of geniculate cells. *Nature, Lond.* **256**, 411–413.