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Functional Classification of Cells in the Optic Tract of a Tree Shrew (Tupaia chinensis)

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The spatial and temporal characteristics of the stimulus-response relationship of retinal ganglion cells in a tree shrew (Tupaia chinensis) have been examined. Tree shrews are generally considered to be rather primitive primates, but there is some discussion regarding their proper taxonomical place (Schwaier, 1973). The retina of the tree shrew contains a great many cones, but few, if any rods (Castenholz, 1965; Dieterich, 1969).

The animals were immobilized with gallamine-triethiodide (Flaxédil) and artificially respired with $N_2 0/0_2$ (2:1). Recordings were made from single optic tract fibres by means of tungsten micro-electrodes. Twenty-six animals were used. Details of the technique are published elsewhere (Laak *et al.*, 1975). In this study 93 units were investigated which could be classified in several groups.

sustained	29
transient	29
on-off	7
suppressed-by-contrast	2
direction-selective	16
orientation-selective	6
opponent-colour	1
edge-inhibitory-off-centre	1
not classified	2
Total	93

Sustained and Transient Cells

Sustained cells respond with a train of action potentials at the on-set or at the off-set of receptive field centre illumination. The duration of this train of action-potentials is as long as the stimulus (Fig. 1A, B). Under the same conditions transient cells respond with a short burst even in the dark adapted situation (Fig. 1C, D) which is in contrast to the findings in the cat (Cleland *et al.*, 1971). In the light

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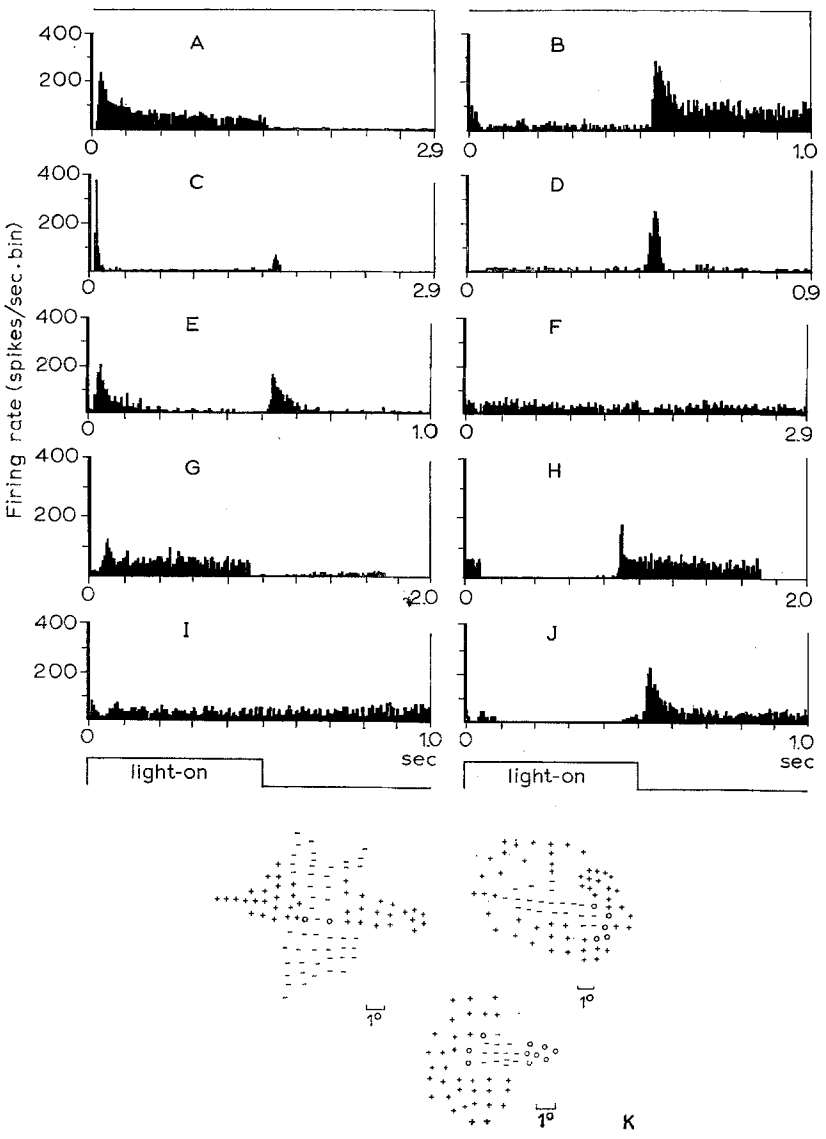

Fig. 1. Post-Stimulus-Time-Histogram (PSTH) of different cell types stimulated by a small central spot. Dark adaptation (A) On-centre sustained. (B) Off-centre sustained. (C) On-centre transient. (D) Off-centre transient. (E) On-off. (F) Suppressed-by-contrast. (G) Opponent-colour, 440 nm stimulus. (H) Opponent-colour, 576 nm stimulus. (I) Edge-inhibitory-off centre, 15′ stimulus spot. (J) Edge-inhibitory-off centre, 1° stimulus spot. (K) Receptive field maps of three off-centre orientation-selective cells in darkness; +: sustained on-response, —: sustained off-response, ○: no response at all, test spot 20′

adapted state illumination of the surround evoked off-responses in on-centre sustained cells while in on-centre transient cells only on-off responses could be evoked (Laak, 1975). The on- and off-responses have different latencies.

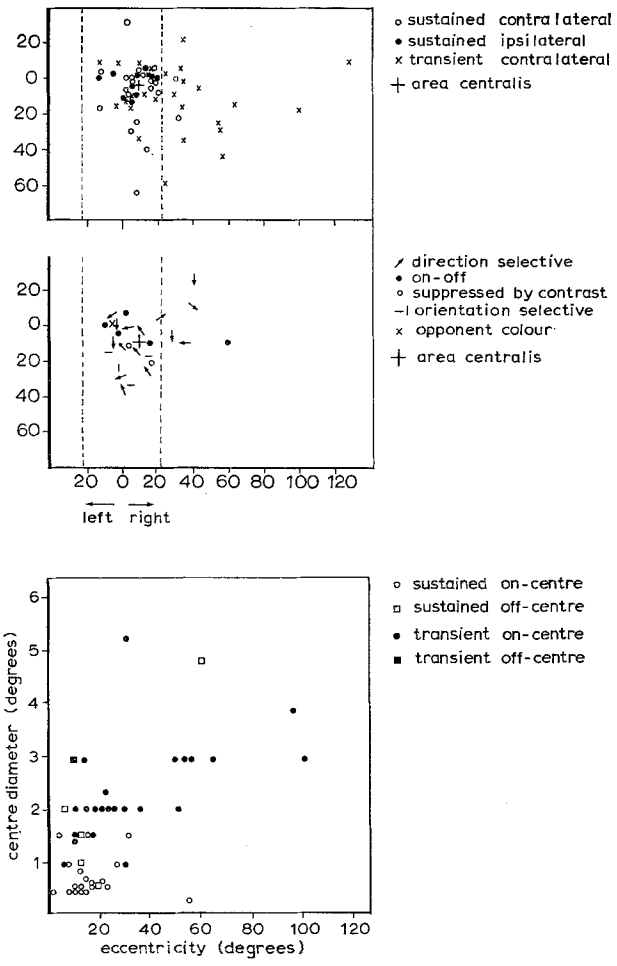

Fig. 2. Localization of receptive fields of fibres in left optic tract. Approximate localization of area centralis of the right eye is indivated by a cross. Visual fields of the eyes overlap between dashed lines. Above: Sustained and transient units. Middle: Other types of cells. Below: Correlation between distance to area centralis and size of the receptive field centres of sustained and transient units in dark adaptation (usually measured with area-response curves)

The sustained cells are grouped around the area centralis whereas the transient cells are spread over the whole retina (Fig. 2, above). The sustained cells have smaller receptive field centres than the transient cells (Fig. 2, below). All transient cells send their fibres to the contralateral hemisphere, while 17 sustained units do cross and 12 do not. In the left optic tract most fibres of sustained units have receptive fields in the right visual field. For other properties of the sustained and the transient cells we refer to separate publications (Laak, 1975; Thijssen *et al.*, 1975).

Sustained and transient cells have also been found in the tree shrew's lateral geniculate body (Sherman *et al.*, 1975).

On-off Cells

On-off cells respond with a burst of action potentials at light-on and at light-off in the receptive field centre (Fig. 1E). The latencies of the on- and off-burst are equal within the measuring accuracy of ± 5 msec and range from 30 to 60 msec depending on the stimulus intensity. In some units the responses to light-on and light-off are almost identical (Fig. 1E). The receptive field size ranges from 1.0° to 2.0°.

Suppressed-By-Constrast Cells

These cells, called suppressed-by-contrast cells according to Rodieck (1967), have a relatively high maintained activity (on the average 14 spikes per second in darkness), which is suppressed at the on-set and at the off-set of a small spot (2°) in the receptive field centre (Fig. 1F). To a larger spot (6°) they do not respond at all.

Direction-Selective Cells

Direction-selective cells respond with a burst of action potentials when a dark or a light stimulus is moved in one direction (the preferred direction) over the receptive field, whereas they show a suppression of their activity while moving the stimulus in the opposite direction (the 'null' direction). The maintained activity in darkness is always less than 3 spikes per second. The localisation of the receptive fields as well as the preferred directions have been plotted in Fig. 2, middle. To stepwise changes in receptive field centre illumination, eight direction-selective cells reacted with on-off, and six with on-responses, and one unit gave no response at all. The receptive fields are large and range from 2° to 6°.

The direction-selective cells, as well as the on-off cells and the suppressed-by-contrast cells, provide a stronger response to small light stimuli than to larger stimuli with the same intensity. Therefore all these types reveal a surround.

Orientation-Selective Cells

Orientation-selective cells have a receptive field with a short and a long axis, the latter is mostly at least twice as long as the former. The cells respond to central illumination with a sustained train of action potentials. The receptive fields of off-centre orientation-selective cells are very large (long axis 2.5° to 8°) and sometimes strangely shaped (Fig. 1K). Off-centre orientation-selective cells respond with a sustained on-train at peripheral illumination in the dark adapted situation. This is in contrast to the sustained cells, where pure surround responses occur only in the light-adapted state. Hence in off-centre orientation-selective cells the on-response mechanism reacts like a centre-response mechanism. At stimulation with a larger spot covering on- and off-regions, the response was vague and irregular. Three on-centre orientation-selective cells have been found, but they are only superficially investigated.

Opponent-Colour Cells

A single opponent-colour cell was encountered. At central illumination it gave sustained on-responses to blue light stimulation and sustained off-responses to red light (Fig. 1G, H). The maximum sensitivity for short wavelengths was at about 440 nm and for long wavelengths at about 560 nm. The reversal point for on- and off-responses was at about 500 nm. This is in accordance with behaviourally measured hue discrimination (Polson, 1968). The receptive field centres of both mechanisms (measured with area-response curves) were equally large (1.2°). The red mechanism had an on-surround, as was demonstrated with a monochromatic far red (656 nm) annulus (2.4°—9.6°) and a small (0.6°) steady central red spot (wavelength above 600 nm). The blue mechanism did not reveal an off-surround.

Edge-Inhibitory-Off-Centre Cells

We found a single cell the activity of which was transiently suppressed when a small spot in the receptive field centre was turned on whereas the cell did not respond at all when that spot was turned off (Fig. 1I). If the area of the spot was a larger one (Fig. 1J), the cell would respond at light-off with a sustained train of action potentials. At light-on the response in this condition was a small transient burst, followed by a suppression of the activity during the whole on-period. Unfortunately we were not able to carry out a more elaborate stimulation program.

Cells Not Classified

A thorough investigation of the two not classified cells was not possible but their response characteristics seemed to be different from the above described cells and from cells reported in the literature.

Comparison with Other Animals

The response characteristics, the receptive field sizes and structure as well as the location at the retina of the various cell types in the tree shrew are much the same as types of ganglion cells described under identical or different names in the cat and somewhat less clear in the rabbit (e.g. Levick, 1967; Winters *et al.*, 1972; Cleland *et al.*, 1971; Cleland and Levick, 1974b; Stone and Fukuda, 1974; Fukuda and Stone, 1974). We cannot decide whether our orientation selective units are of the same type as the units with a more or less elongated receptive field described by other authors in rabbit and cat (Levick, 1967; Cleland and Enroth-Cugell, 1968). The response characteristics of units in the tree shrew are rather different from those of units described in the rhesus monkey (Monasterio and Gouras, 1975). We did not investigate the conduction velocity nor the projection area of the fibres, so we do not know whether the cell types in the tree shrew have in this regard the same properties as the comparable types in the cat (e.g. Fukuda and Stone, 1974). Maybe the great portion of units other than sustained and transient ('W-cells?') coheres with a very large superior colliculus in the tree shrew. We have not investigated whether our sustained and transient units form two homo-

geneous groups, or a distinction must be made between brisk and sluggish units (Cleland and Levick, 1974a; Stone and Fukuda, 1974).

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