

CAT RETINAL GANGLION CELLS: SIZE AND SHAPE OF RECEPTIVE FIELD CENTRES

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SUMMARY

1. Receptive field centres of 144 sustained and transient retinal ganglion cells were mapped in cats under light pentobarbitone anaesthesia.

2. Sustained on-centre, sustained off-centre, transient on-centre and transient off-centre cells had different mean sizes of receptive field centre, with some overlap between their distributions.

3. For each class of cell, central fields had the smallest field-centres; progressively larger field-centres were encountered more peripherally.

4. All classes of ganglion cells tended to have slightly elliptical receptive field centres. Major axes of over half of all receptive fields were oriented within 20° of horizontal. These trends were independent of pupil dimensions, or of receptive field eccentricity or position in the visual field. The results almost certainly reflect asymmetry in retinal wiring.

5. Two cells of thirty-nine tested were sensitive to axis of motion; in both cases the preferred and major axis were horizontal. A further cell was orientation specific.

INTRODUCTION

On-centre and off-centre ganglion cells in the cat's retina, with receptive fields incorporating concentric but antagonistic central and peripheral zones, were first described by Kuffler (1953). These cells have either 'sustained' or 'transient' characteristics (Enroth-Cugell & Robson, 1966; Cleland, Dubin & Levick, 1971; Fukada, 1971; Cleland & Levick, 1972; Ikeda & Wright, 1972; Cleland, Levick & Sanderson, 1973) and are wired to both cones and rods, with super-imposed receptive fields for each class of receptor (Barlow, Fitzhugh & Kuffler, 1957; Andrews & Hammond, 1970*a, b*; Hammond, 1973*a*).

In the cat's peripheral retina, with the exception of the recently discovered W-cells, non-concentric receptive fields are conspicuous by their rarity (Rodieck & Stone, 1965*a*; Rodieck, 1967; Ogawa, Bishop & Levick, 1966; Barlow & Levick, 1969; Andrews & Hammond, 1970*a, b*; Hammond & James, 1971; Cleland *et al.* 1971). Specialized types may however be

more common within the area centralis (Stone & Fabian, 1966). Spinelli's (1966*a, b*) claims of a diversity of types of cat ganglion cell receptive fields remain unsubstantiated, and have been challenged by Barlow, Levick & Westheimer (1966).

A commonly held view is that the receptive fields of on-centre and off-centre ganglion cells approximate to radial symmetry. In practice their fields are frequently elliptical rather than circular and the most sensitive point within the receptive fields may be located well away from the geometric centre (Kuffler, 1953; Rodieck & Stone, 1965*b*). Correspondingly, the dendritic fields of cat ganglion cells, generally associated with receptive field centres (Brown & Major, 1966; Dowling & Boycott, 1966; Honrubia & Elliott, 1970; Boycott & Wässle, 1974), are irregular in outline and often asymmetrical in spread (Leicester & Stone, 1967; Honrubia & Elliott, 1970; Boycott & Wässle, 1974),

The size and shape of receptive field centres of on-centre and off-centre ganglion cells in the cat's peripheral retina were therefore re-examined. Three features were of particular interest. Firstly, the relationship between field-size and ganglion cell class; secondly, the possibility of a systematic relationship between receptive field centre shape and visual field location thirdly, the possibility that receptive field asymmetry might be consistent with slight but predictable sensitivity to axis of motion.

METHODS

Preparation. Ten adult cats (range 1.9–3.8 kg, mean 2.7 kg), were prepared for recording under pentobarbitone anaesthesia (Nembutal, Abbott). Left and right cephalic veins and the trachea were cannulated. Rectal temperature was maintained at 38 °C. Blood pressure and pulse were monitored continuously with a Devices/CEC pressure transducer attached to a cannula in the left carotid artery, kept patent by slow infusion of 3% (w/v) sodium citrate solution at about 0.3 ml./hr. The surface-cortical e.e.g. (bandpass 0.8–50 Hz) was monitored throughout between screw-electrodes over the left striate and auditory cortices. At an early stage force-ventilation at 28 strokes/min and 3.8% end-tidal CO₂ was applied, to ensure stable gas exchange; CO₂ levels were measured with a Beckman LB-1 Medical Gas Analyser. The animal was mounted in a Narishige stereotaxic frame with rounded ear bars, modified to permit removal of the orbital bars after the initial positioning in the head holder. Scalp and temporales muscles were reflected and a small craniotomy, centred vertically above the right optic tract, was performed.

Surgery complete, pentobarbitone anaesthesia was allowed to lighten as far as was judged to be consistent with satisfactory anaesthesia on reflex and other conventional criteria. Records of e.e.g., blood pressure and pulse, end-tidal CO₂ and rectal temperature were assessed together as indicators of anaesthetic adequacy after paralysis. Animals were paralysed with 2 ml. of a 50:50 mixture of Flaxedil (May and Baker, at 40 mg/ml.) and 5% dextrose given i.v., followed by continuous i.v. infusion of the same mixture at 1 ml./hr (20 mg Flaxedil/hr). Anaesthesia was maintained by frequent small i.p. doses of Nembutal (averaging around 3 mg.kg⁻¹.hr⁻¹).

Pupils were dilated with 1% (w/v) atropine sulphate, and the eyelids and nictitat-

ing membranes retracted pharmacologically with 10% (w/v) phenylephrine hydrochloride. Two animals were provided with 3 mm diameter (7 mm²) artificial pupils, carefully centred in front of the natural pupils and placed as close as possible to each cornea. The orbital bars of the stereotactic instrument were placed by clamps on the frontal bones to facilitate positioning of the artificial pupils. The corneae were protected with two-curve neutral contact lenses, selected from three pairs according to body weight (Andrews & Hammond, 1970*a*). The eyes were refracted for focus in the plane of a matt white, translucent tangent screen at a distance of 57.3 in. from the anterior nodal points, and focal correction was achieved with 38 mm-diameter trial lenses placed as close as possible to each eye. The eye separation for cats within the above weight range was less than 38 mm, and a specially designed trial frame permitted overlap of the lenses at the midline. Locations of each optic disc and area centralis were regularly monitored by back-projection onto the tangent screen, using an ophthalmoscope and cube corner prism. Drift was slight and regular. The maximum drift seen over the 20 hrs or so of recording was 3° for one eye of one animal; drift in most cases was around 1–1.5° over this period.

Estimation of natural pupil size. Two conscious and unoperated cats (2.5 and 3.0 kg respectively) faced a large and uniformly illuminated matt white tangent screen. Luminance was the same as for the single unit experiments (1.24 log cd/m²), and the screen subtended approximately 110° horizontally and 120° vertically.

On each of two occasions, several photographs of each animal's eyes were taken from behind the centre of the screen, with the aid of electronic flash, when the animal's eyes were as nearly as possible in the same plane as a calibrated scale and when they appeared to be looking directly at the camera lens. Width, height and area of the pupils were measured in each case from the photographic enlargements.

Recording. Extracellular records were obtained from single fibres in the right optic tract, posterior to the optic chiasma, with 2.7 M-KCl micropipettes (impedance range 10–30 MΩ). Sixteen successful vertical penetrations were made between Horsley-Clarke stereotaxic co-ordinates A 10.2–9.0, RL 6.5–8.7, to a depth of approximately 2 cm. The craniotomy was sealed with 2% (w/v) immuno-agar (Oxoid) in 0.9% saline, pre-cooled to about 39 °C and the agar plug was coated with low melting point (39 °C) wax to prevent dehydration. Signals were amplified, displayed oscillographically, and stored on FM magnetic tape for analysis at leisure. Spikes could be picked-off with a window-discriminator, converted to standard pulses, and further processed by Nuclear Chicago 7100 or Biomac 1000 special-purpose computers for evaluation of averaged post-stimulus time histograms (PSTHs). Standard pulses were also fed to a variable time constant rate-meter, and to electronic counters with independently controlled gate duration and delay. The raw signal, or the discriminated spikes, could be monitored aurally.

For the axis sensitivity measurements, the gated counts were stored on Dec-tape and also processed on-line by a PDP-8 computer, for evaluating means, standard deviations and standard errors.

Visual stimuli. Achromatic stimuli were produced by two identical tungsten projection systems (Andrews & Hammond, 1970*a*). Stimuli were projected onto the tangent screen against a uniform, achromatic background at 1.24 log cd/m² (near-photopic; Hammond & James, 1971) provided by banks of tungsten filament lamps (Hammond, 1972). A deep red (650 nm) graduated 'cross-wire' image produced by a third projector provided a reference for accurate location of stimuli. This reference was sub-threshold for cat neurones yet clearly visible to a human observer.

Preliminary analysis

Receptive field classification. The position of each receptive field was roughly located and the type of unit (on-centre or off-centre) and driving eye were determined. It was sometimes beneficial to reduce the adapting luminance during the search for off-centre units. Location of receptive fields of transient units was hampered by the periphery effect, which could frequently be obtained even when the centre of the field was beyond the confines of the tangent screen.

Location and dimensions of receptive field centres. Care was taken to locate precisely the most sensitive point within the receptive field, by comparing the gated spike counts for a small spot of light presented for 200 msec/sec. Approximate dimensions of receptive field centres were rapidly estimated with the same stimulus, oscillated in turn across the upper, lower, left and right boundaries. The optimal size was also determined.

Distinction between sustained and transient units. Four tests, described in detail by Cleland *et al.* (1971), provided unequivocal classification of every unit with the exception of one orientation specific unit.

(a) Response to a small centred spot of light of optimal size, presented for 30 sec/min. Only in sustained units was the maintained firing rate changed throughout illumination. Diffuse illumination was not a valid test.

(b) Sustained units had smaller receptive field centres than transient units, and preferred smaller targets. Within each group, on-centre units had smaller field centres than off-centre units.

(c) Transient units responded to higher velocities of movement than sustained units.

(d) The periphery effect could be readily elicited from transient units by a stimulus oscillating several times a second at a considerable distance from the centre of the receptive field. No periphery effect was seen for sustained units.

RESULTS

Receptive field centre maps

Mapping technique. Receptive field centres were mapped on sheets of matt white paper attached to the tangent screen. Threshold for the most sensitive point within each field was determined, using the smallest spot of light consistent with a clear-cut discharge from the unit. Stimulus spots were 0.25, 0.5 or 0.75° in diameter, depending on the class of unit and size of receptive field under investigation. Estimates of threshold were based on combined visual and auditory cues, on comparisons of gated counts for identical periods of firing during and following each stimulus, or on averaged PSTHs. The method chosen depended on the type of unit and its level of maintained firing, the second method being most useful for units with brisk maintained activity.

Next, stimulus intensity was increased ten-fold, and between twelve and twenty threshold points around the perimeter of the receptive field centre were established in random order, using the same stimulus and threshold criteria. All these points thus lay on a contour of iso-sensitivity, and with

practice it proved possible to repeat determinations to within $\pm 0.02^\circ$. Finally the most sensitive point in the field was marked on a line drawn vertically through it.

Receptive field centre maps. Receptive field centre maps were corrected for the distortion introduced by plotting on a tangent screen. The corrected maps of ninety-five units, recorded from animals with dilated pupils, are shown in Fig. 1. Of these units, sixty-two were sustained – forty-three sustained on-centre (S +), nineteen sustained off-centre (S –); thirty-three were transient – twenty-two transient on-centre (T +), eleven transient off-centre

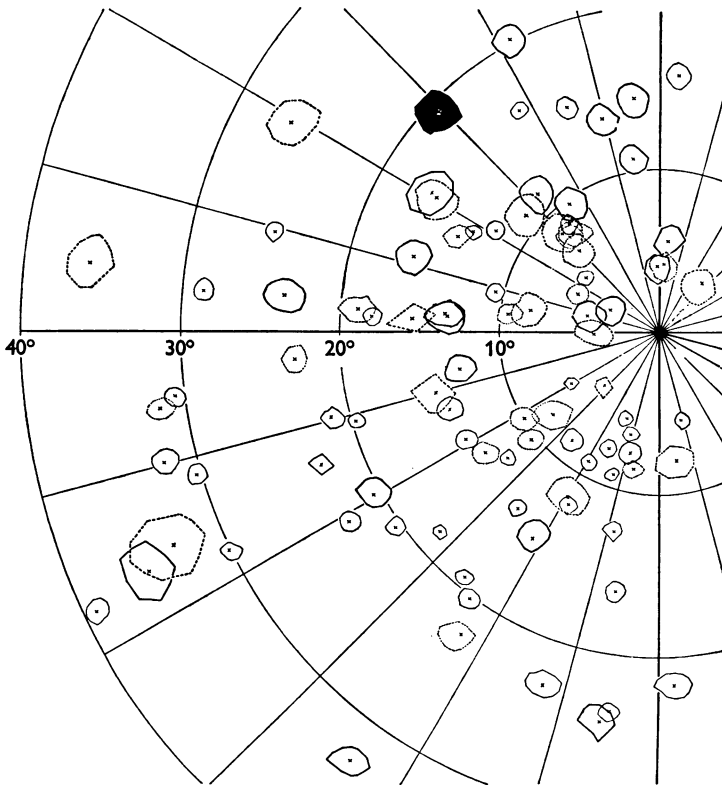


Fig. 1. Outlines of unit receptive field centres and their locations in the visual field. Each cross marks the most sensitive point within a receptive field. *Sustained units* – thin profiles; *transient units* – bold profiles; *on-centre units* – continuous profiles; *off-centre units* – dashed profiles. The scale gives angular eccentricities in degrees from the projection of the area centralis. Data for the two eyes appear on the same diagram, and a position angle of 25° is assumed between each area centralis and the respective optic disk (Bishop, Kozak & Vakkur, 1962). The shaded profile is for a contralaterally-driven, transient on-centre unit, imaged from its true location in the right half of the visual field.

(T-). The different classes of unit are distinguished in the Figure by width and continuity of outline. Because of limitations of scale, plotted loci are occasionally masked by an apparently single straight contour.

TABLE 1. Receptive field centre dimensions for the various functional classes of ganglion cell. Values given are the mean and s.e. of mean. Note that one S+ unit is excluded from the figures for orientation of the major axis

Unit class	S+	S-	All S	T+	T-	All T	All
Numbers of units (<i>n</i>)	43	19	62	22	11	33	95
Length of major axis (degrees)	1.30 ± 0.05	1.95 ± 0.11	1.50 ± 0.06	2.30 ± 0.09	2.90 ± 0.27	2.50 ± 0.11	1.85 ± 0.07
Length of minor axis (degrees)	1.10 ± 0.04	1.52 ± 0.10	1.23 ± 0.04	1.88 ± 0.08	2.27 ± 0.19	2.01 ± 0.09	1.50 ± 0.06
Ratio	1.18 ± 0.02	1.30 ± 0.03	1.22 ± 0.02	1.23 ± 0.03	1.30 ± 0.08	1.25 ± 0.03	1.23 ± 0.02
Length of radial axis (degrees)	1.18 ± 0.04	1.67 ± 0.10	1.33 ± 0.05	2.10 ± 0.07	2.63 ± 0.26	2.28 ± 0.10	1.66 ± 0.07
Length of tangential axis (degrees)	1.17 ± 0.05	1.61 ± 0.11	1.31 ± 0.05	1.99 ± 0.10	2.38 ± 0.23	2.12 ± 0.10	1.59 ± 0.06
Ratio	1.02 ± 0.02	1.06 ± 0.05	1.04 ± 0.02	1.08 ± 0.04	1.13 ± 0.07	1.10 ± 0.03	1.06 ± 0.02
Length of horizontal axis (degrees)	1.26 ± 0.05	1.90 ± 0.11	1.46 ± 0.06	2.19 ± 0.09	2.66 ± 0.23	2.35 ± 0.10	1.77 ± 0.07
Length of vertical axis (degrees)	1.16 ± 0.04	1.54 ± 0.09	1.28 ± 0.04	2.01 ± 0.09	2.37 ± 0.20	2.13 ± 0.09	1.57 ± 0.06
Ratio	1.09 ± 0.02	1.24 ± 0.04	1.14 ± 0.02	1.11 ± 0.04	1.15 ± 0.07	1.12 ± 0.03	1.13 ± 0.02
Orientation of major axis (degrees clockwise from vertical)	86.1 ± 6.4 (<i>n</i> = 42)	83.9 ± 7.5	85.4 ± 4.9 (<i>n</i> = 61)	100.7 ± 9.3	87.7 ± 12.8	96.4 ± 7.4	89.3 ± 4.1 (<i>n</i> = 94)
Eccentricity (degrees)	16.9 ± 1.3	12.4 ± 1.7	15.5 ± 1.1	15.6 ± 1.8	15.6 ± 3.6	15.6 ± 1.7	15.5 ± 0.9

Units driven by left or right eyes showed no differences in their properties, but without exception every unit with a receptive field straddling the vertical meridian, or in the right (ipsilateral) half of the visual field, was driven by the contralateral (left) eye. This trend is consistent with our earlier investigations (Andrews & Hammond, 1970*a, b*; Hammond & James, 1971; Hammond, 1973*a*). The shaded profile is for a contralaterally driven T+ unit with its receptive field located well into the ipsilateral visual field, and in construction of the Figure this field has been translated across the midline.

All measurements taken from the corrected field centres are shown in Table 1. Unless otherwise stated, the *t* test has been used for statistical comparisons based on these measurements.

Receptive field centre size. Because all receptive field centres with one exception showed some degree of asymmetry (Fig. 1), the length of the

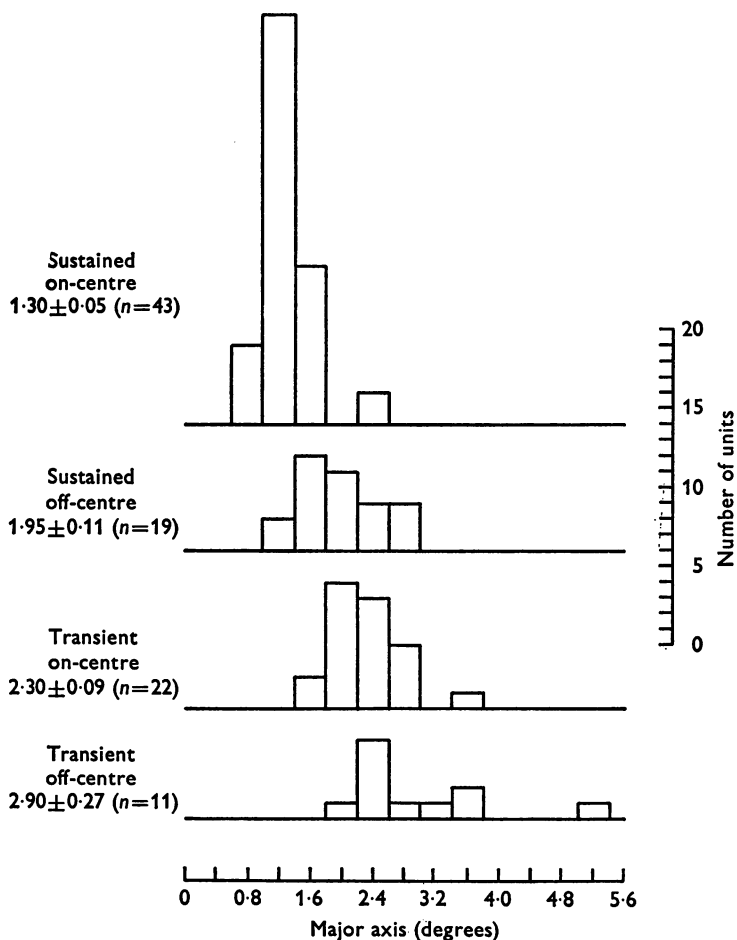


Fig. 2. Receptive field centre size: dimensions of major axes are compared for the different classes of unit. The mean and s.e. in degrees, together with the number of units in each class, are shown on the left.

major (longest) axis was chosen to compare their size (Fig. 2). This axis was estimated by eye, without knowledge of the orientation of each receptive field in visual space. It can be seen from Fig. 2 that different classes of unit had different sizes of receptive field centre. The dimensions

of major axes for sustained and transient units (Table 1) were significantly different ($P < 0.001$). Similarly the mean for on-centre units ($1.64 \pm 0.07^\circ$, $n = 65$) was less than for off-centre units ($2.30 \pm 0.14^\circ$, $n = 30$). Within the sustained and transient groups, S+ units had the smallest field centres, and T- units the largest field centres. There were comparable differences between measurements for the minor axis (Table 1), orthogonal to the major axis.

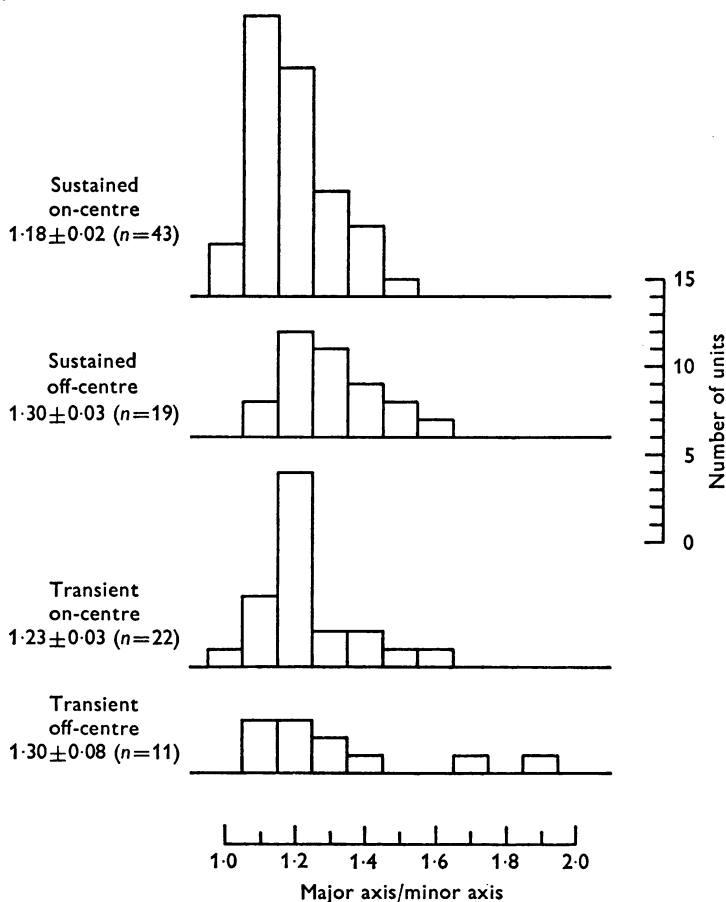


Fig. 3. Receptive field centre *shape*. Distributions of the ratios of major to minor axes are compared for the different classes of unit. The mean, s.e., and number of units in each class are shown on the left.

Because field centre size varies with eccentricity (see Fig. 4 and below), it may be thought that these size differences are caused by differences in the eccentricity of different types. However, this is not borne out by the results (Table 1; Figs. 1 and 4), since means and distributions of eccentricity

city of receptive fields were similar for each of the four classes of cell and there was no evidence to suggest that transient cells were more common in the periphery. In Figs. 2 and 4 it is also worth noting that the two **S+** units, and the three **S-** units, which had the largest receptive field centres represented the total sample from one animal. These units were unequivocally sustained, but if one rejects them as atypical the definition between the different classes of unit is significantly improved.

Receptive field centre shape: departures from radial symmetry. Shapes of receptive field centres were estimated by comparing the lengths of the major and minor axes for each unit (Fig. 3). Any symmetry in receptive field centre shape may simply reflect random variations from radial symmetry (a unimodal distribution with mean ratio equal to unity), due to imperfections in neural connectivity. Alternatively, there may be a *systematic* bias towards elliptical rather than circular fields (a bimodal distribution). The chi-squared test was therefore used to compare the observed distribution of *log* ratios with a normal distribution centred about zero (on a *log* scale). Since the measured ratios were always defined as major/minor axis, the values can be treated as one half of the overall distribution. For all sustained and transient units, χ -squared gave $P < 0.002$. The distribution was clearly bimodal, which is in favour of a *systematic* bias towards elliptical receptive fields. The distributions and means for the *log* ratios of major to minor axis were similar for **S+**, **S-**, **T+** and **T-** classes. Boycott & Wässle (1974) observe that major and minor axes of dendritic fields of cat retinal ganglion cells 'usually differed by between 10 and 20 %, occasionally the difference was as much as 30 %.' Comparable differences are to be seen in Fig. 3 for ganglion cell receptive field centres.

Receptive field centre size and shape: correlation with eccentricity and location in the visual field. Linear regression analysis confirmed that cells with peripheral receptive fields have larger field centres than those near the centre of the visual field. Length of major axis was correlated with eccentricity (Fig. 4). The slopes were positive in each case and deviated significantly from zero (**S+** units, $P < 0.002$; **T+** and **T-** units, $P < 0.001$) except for **S-** units for which the scatter was high. The range of receptive field centre size, and the variation of centre size with eccentricity, compare favourably with direct measurements of dendritic trees of β and α cat retinal ganglion cells which are described by Boycott & Wässle (1974).

Linear regression analysis of the *log* ratio of major/minor axis *vs.* eccentricity for each class showed that, with the exception of a weak correlation in the case of **S-** units ($P < 0.05$), receptive field centre shape was independent of eccentricity.

There was no correlation between the location of each receptive field in

visual space and the orientation of its major axis. Mean lengths of the radial, and orthogonal tangential, axes were similar. (By definition, the radial axis lies on the visual field radius which passes through the centre of the receptive field.)

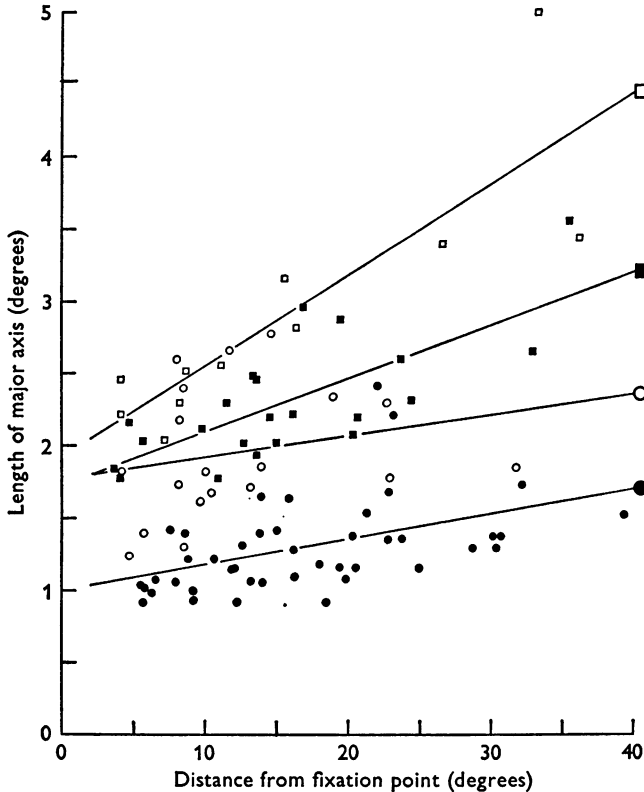


Fig. 4. Comparison between length of major axis and eccentricity of a receptive field centre, for the various classes of unit: S+ units ●; S- units ○; T+ units ■; T- units □. Regression lines are fitted for each group.

However, more than half of all receptive fields had major axes oriented within $\pm 20^\circ$ of horizontal. The distribution is illustrated in Fig. 5. (Note that this polar diagram is not a plot of orientation selectivity.) The mean orientation for all units was $89.3 \pm 4.1^\circ$ ($n = 94$, excluding one radially symmetrical field). Fig. 6 shows that the relationship holds for every class of unit; mean orientations for all groups were similar and close to horizontal. Horizontal axes through each receptive field centre tended to be longer than vertical axes. The mean lengths and ratios for each class of cell are given in Table 1.

Controls for pupils size

The receptive fields just described were measured in cats with fully dilated pupils. It is therefore possible that the bias for horizontal may have reflected artificially induced optical aberrations, particularly since the cat's normal pupils tend to be slit-shaped and almost vertical. The S+ cells (those most numerous in the foregoing data) were therefore compared with a further sample of 49 S+ cells, obtained from two cats fitted with 3 mm diameter artificial pupils (see Table 2).

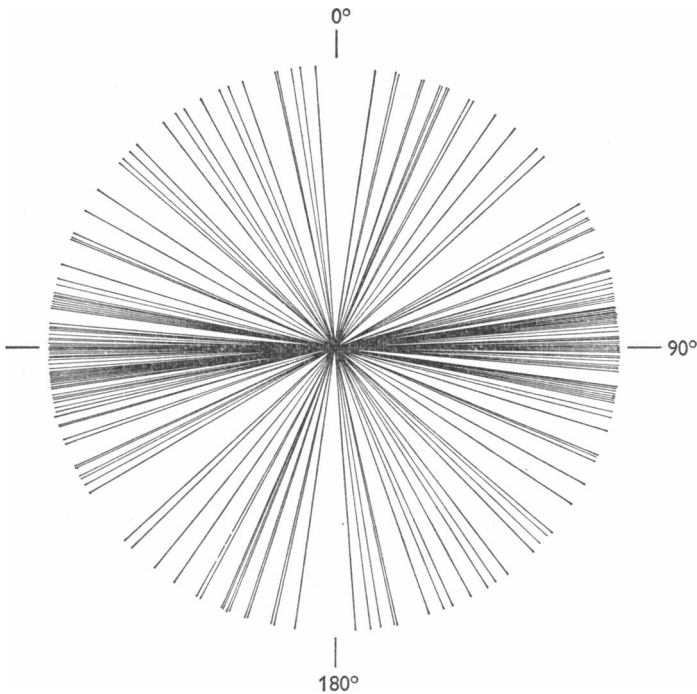


Fig. 5. Orientations of major axes for the receptive field centres of all units ($n = 94$), showing a clear preference for horizontal. One sustained unit with a precisely circular field is excluded.

The distributions of receptive fields in the left half of the visual field were comparable for the two groups of units, and their mean eccentricities were similar.

Distributions and means for length of major axis, ratio of major to minor axis, and orientation of major axis for the two groups of units are compared in Fig. 7. The distributions of receptive field centre size were similar for each group and increased with retinal eccentricity. Distribu-

tions for receptive field centre shape were also similar, and uninfluenced by retinal eccentricity. In each group, the major axes of almost half the units were oriented within 20° of horizontal.

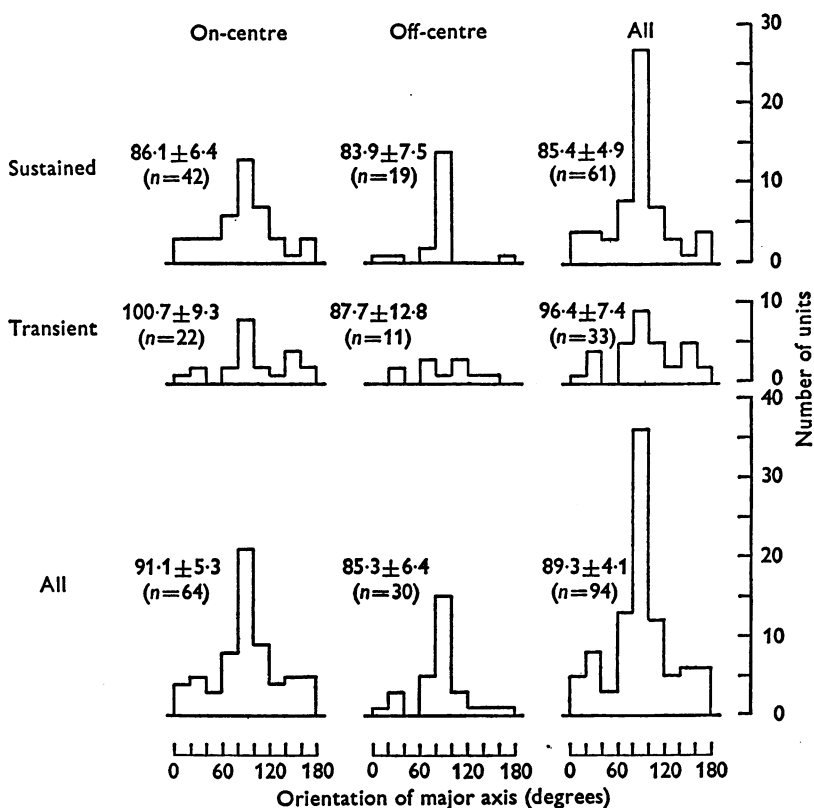


Fig. 6. Distribution of orientations of major axes for the receptive field centres of the various classes of unit. The horizontal preference is preserved for all groups.

Dimensions of natural pupils

Photographs of the mobile pupils from two conscious cats were rejected if the animals were clearly not looking at the camera lens, or if the eyelids partially obscured the pupils. Pupil dimensions were roughly the same for left and right eyes and for each animal. All satisfactory data were therefore pooled (eight measurements from the smaller, and four measurements from the larger animal).

At $1.24 \log \text{cd/m}^2$ the pupils were in fact comparatively widely dilated and only slightly elongated vertically. Mean measurements were: width 8.7 mm (range 7.4–9.7 mm); height 9.9 mm (range 9.3–10.4 mm); and area 62 mm^2 (range 53–71 mm^2).

The original intention was to map ganglion cell receptive field centres in these cats under anaesthesia, using suitable artificial slit pupils. These experiments were clearly unnecessary, in view of the large size and approximately circular shape of the natural pupils.

TABLE 2. Comparison of receptive field centre dimensions for sustained on-centre ganglion cells, obtained with dilated natural pupils and 7 mm² artificial pupils respectively. Figures given are means and s.e. of the means

Pupil dimensions	Dilated	3 mm diameter
Number of units (<i>n</i>)	43	49
Length of major axis (degrees)	1.30 ± 0.05	1.33 ± 0.05
Length of minor axis (degrees)	1.10 ± 0.04	1.14 ± 0.05
Ratio	1.18 ± 0.03	1.17 ± 0.02
Length of radial axis (degrees)	1.18 ± 0.04	1.23 ± 0.05
Length of tangential axis (degrees)	1.17 ± 0.05	1.18 ± 0.05
Ratio	1.02 ± 0.02	1.04 ± 0.02
Length of horizontal axis (degrees)	1.26 ± 0.05	1.26 ± 0.05
Length of vertical axis (degrees)	1.16 ± 0.04	1.19 ± 0.05
Ratio	1.09 ± 0.02	1.06 ± 0.02
Orientation of major axis (degrees clockwise from vertical)	86.1 ± 6.4 (<i>n</i> = 42)	87.3 ± 7.2
Eccentricity (degrees)	16.9 ± 1.3	16.1 ± 1.2

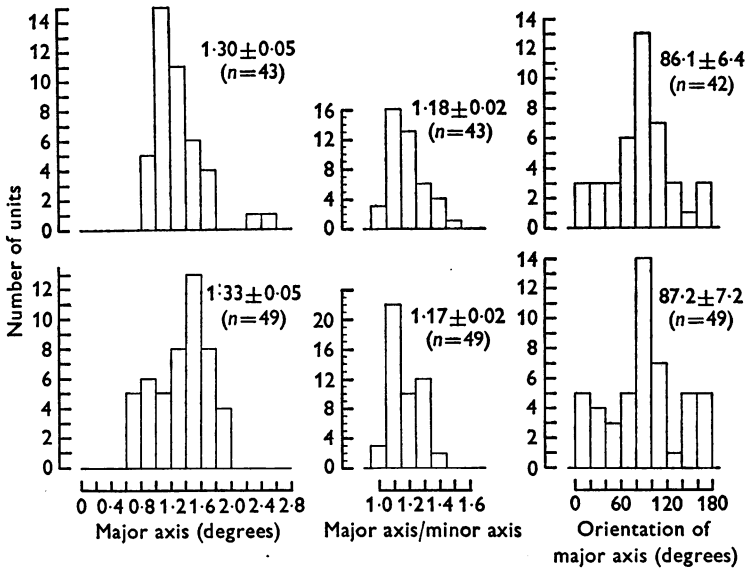


Fig. 7. Comparison of lengths of major axes, ratios of major/minor axes, and orientations of major axes for groups of S+ units with dilated natural pupils (upper row) or 7 mm² artificial pupils (lower row). Means, s.e. of means and numbers of units in each group are given.

Sensitivity to axis of motion

Technique. Stimuli were moved back and forth along different axes through each receptive field centre. Intensity was within one log unit of threshold. The stimulus moved at $10^\circ/\text{sec}$ through an angular distance of 10° , and excursion was centred over the most sensitive point in the field. Small spots of light were used in the early experiments. Since the path followed by such stimuli was extremely critical an 11° -long slit of light of optimal width, oriented perpendicular to the axis of motion, was used in all later experiments.

Axis of motion was defined as follows: 0° = upward followed by downward motion; 90° = horizontal motion to the right, followed by movement to the left; 180° = downward followed by upward movement.

Responses of on-centre and off-centre units to motion were similar to those described by Rodieck & Stone (1965*a*) for positive contrast stimuli. Suitably gated discharges were counted for each direction of motion, as the stimulus passed through the field centre of on-centre units, or left the field centre and simultaneously entered the periphery of off-centre units.

As a check on unit consistency, axes were tested at 40 or 45° intervals between 0 and 180° , filling in the intermediate axes in reverse order. Maintained firing was compared before and after each run.

Axial sensitivity. Measurements were obtained from thirty-nine units, and receptive field maps were also obtained for eleven of these. Incomplete data were obtained from a further twenty-one units. The majority of units (thirty-seven out of thirty-nine) were insensitive to the axis of motion.

Two units showed a systematic preference for horizontal movement, although there was still a brisk response to vertical movement. One of these, illustrated in Fig. 8, consistently gave about fifty spikes for a horizontal traverse through the receptive field, compared with about 35 spikes for a vertical traverse and a maintained discharge of around seven spikes in the same gated period. No unit showed any directional preference. Both units had markedly elliptical receptive field centres. The ratio of horizontal/vertical axis was 1.47 for the unit illustrated, and approximately 1.75 for the second unit. Thus the axial preference presumably reflects the greater duration of excitation for the horizontal traverse, as can in fact be seen from PSTHs.

Exceptional case: orientation-specific unit. One fibre is worthy of note because its properties were so unusual. The unit was isolated during a sequence of sustained and transient units with conventional centre-surround fields. It was held comparatively briefly, was driven only by the contralateral eye, and showed orientation-specificity more akin to that of cells in striate cortex. It fired transiently to a narrow vertical stripe, or to

small spots of light, flash-presented over a narrow vertically elongated zone. It responded well to horizontal movement of a vertically oriented stripe, or to small targets moved horizontally over a wide range of elevations. The unit was totally unresponsive to obliquely- or horizontally oriented slits, whether moving or flash-presented. The receptive field was situated almost exactly over the vertical meridian of the visual field, extending inferiorly from a few degrees below the projection of the area centralis.

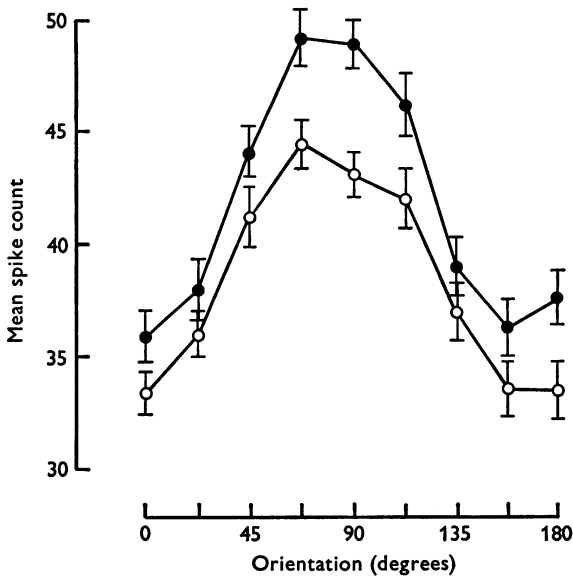


Fig. 8. Axial sensitivity of a transient on-centre retinal ganglion cell. The stimulus was a 1° spot of moderate contrast, moved back and forth through the centre of the receptive field at a velocity of $10^\circ/\text{sec}$, over an angular subtense of 10° . The limits given are ± 1 s.e. of the mean, for twenty consecutive trials at each orientation. Filled and open symbols are for opposite directions of movement (forward and reverse), obtained simultaneously along each axis. Movement along axes, in degrees clockwise from vertical, were tested in the following order: 0, 45, 90, 135, 180, 157.5, 112.5, 67.5, 22.5°.

DISCUSSION

The results indicate a slight preference for horizontal in the cat's retina and it is worth noting Stone's (1965) observation of a 'horizontally oriented arm (of ganglion cells) of relatively high density extending from the central area into nasal and temporal retinae'. The receptive field asymmetries are slight compared with higher order visual neurones; what is significant is that at the retinal level they occur in a systematic fashion at

all. An overall ordered pattern of retinal receptive field shape may have important consequences for perception.

There is also evidence for horizontal preference elsewhere in the visual system. In the superior colliculus, cells prefer movement away from the centre of gaze (Straschill & Hoffmann, 1969; Sterling & Wickelgren, 1969) or horizontal movement away from the vertical meridian (Berman & Cynader, 1972). Activating regions of collicular receptive fields increase in size with distance from the area centralis and virtually all are horizontally elongated.

In the striate cortex there is much support for all orientations being represented with equal frequency (Hubel & Wiesel, 1962; Campbell, Cleland, Cooper & Enroth-Cugell, 1968; Pettigrew, Nikara & Bishop, 1968). But Pettigrew and colleagues (1968) note that directionally-selective unimodal simple units prefer vertical and horizontal orientations. Because of the cortical orientation columns, small samples of cells may show appreciable bias (e.g. Hammond, 1971), but in accumulated data for over six hundred cortical cells Bishop and colleagues still find a clear preference for horizontal and vertical and slight preference for 135°-diagonal orientations (P. O. Bishop, personal communication).

Even in the lateral geniculate nucleus, 'most of the units respond differently to movement along different radii', due to 'slight lack of symmetry in the distribution of excitatory and inhibitory regions'; receptive fields are frequently on-off, directionally-sensitive, or diffuse (Kozak, Rodieck & Bishop, 1965). Fukada & Saito (1973) have also observed directionally-selective units in LGN, although these were not driven monosynaptically by ganglion cell axons and may have been cortico-geniculate fibres.

At least five factors may contribute to the clustering of major axes of ganglion cell receptive fields about horizontal.

1. Residual errors, *not corrected by* accessory optics.
2. Errors *introduced by* accessory optics.
3. Aberrations caused by pupil size.
4. *Inherent* aberrations in the cat's natural optics.
5. Genuine differences in neural connectivity.

The present experiments almost certainly rule out the first four alternatives.

All the stimuli were threshold or near-threshold spots of light, presented against near-photopic backgrounds, and light scatter is unlikely to have presented serious problems. Several factors indicate that the shapes of retinal receptive fields were not influenced appreciably by optical aberrations peculiar to each experimental animal, by imperfections in accessory optics, or by pupil size. In the experiments with dilated pupils, receptive

field shapes were similar for all classes of unit and did not vary with eccentricity in the visual field. One might expect distortions in receptive field shape to be more pronounced peripherally than centrally. In particular, the absence of systematic elongation of receptive field centres along radial axes almost certainly rules out coma.

Appropriate spherical corrections were made for all animals and neutral contact lenses of suitable curvature, fitted primarily to prevent corneal drying, effectively compensated for astigmatism caused by irregularities in the corneal surface. No cylindrical correction was made and astigmatic imaging would also have occurred in all cats for off-axis stimuli, but it is improbable that every animal suffered similar defects by chance, or that the external optics always introduced precisely the same aberration. The prevalence of near-horizontal major axis orientations was obvious for all animals and the shapes of receptive fields were similar for each animal. Trends in receptive field shape were independent of which was the driving eye, and there appeared to be no tendency for sequentially recorded units, or units referred to a particular sector of the visual field, to have common receptive field shape or major axis orientation. Neighbouring receptive field centres in visual space were often elongated along quite different axes.

It is well known that large pupils increase the blur of the retinal image (Campbell & Green, 1965; Bonds, Enroth-Cugell & Pinto, 1972) but in cats there is no evidence to suggest that any distortion results (Wässle, 1971). An artificial stop in front of the animals' own dilated pupils, whilst reducing spherical aberration, coma and curvature of the retinal image, may at the same time introduce distortion since it cannot lie in the same plane as the lens. Against this is the evidence that introducing a 3 mm diameter artificial pupil (as opposed to a fully dilated pupil) actually had no measurable effect on the shape, size and orientation of retinal ganglion cell receptive field centres. (To be on the safe side the results with 3 mm pupils were obtained from two separate animals, and each showed similar trends.) One could argue that the optics might have been further improved by using even smaller artificial pupils, or even an artificial slit pupil. However, such improvement is unwarranted because the natural pupils of conscious cats are approximately circular and substantially greater than 7 mm² in the area at the light levels which were used for mapping receptive fields in the anaesthetised preparations. Experimentally induced errors apart, the results are also inconsistent with there being defects *inherent* in the cats' natural optics. This conclusion follows from much of what has already been stated above, and in particular from the fact that receptive field centre shape was not influenced by enormous variation in pupil dimensions over a range amply embracing the *natural* pupil size which obtains at the light levels used for mapping receptive fields.

It is of course difficult to assess the optical quality of the retinal image by direct examination from the front of the eye, since incident and returning light rays will each suffer aberrations, and no general treatment of aberrations in optical systems employing non-circular stops (such as the cat's pupil) seems to be available. Intuitively, however, it seems improbable that the refracting components of the cat's optics, alone or in combination, could adequately compensate the retinal image for receptive field asymmetries of the order measured.

In conclusion, the results favour systematic asymmetry in retinal wiring and the possibility that the shape and axial or orientational preferences of receptive fields of higher order visual neurones may be at least partially pre-determined within the retina cannot be ruled out. An outside possibility is that retinal neural connectivity may also be conditioned by visual experience, although it is improbable that all the animals in the present series were selectively exposed in early life to environments rich in contours of similar orientation.

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