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BRISK AND SLUGGISH CONCENTRICALLY ORGANIZED GANGLION CELLS IN THE CAT'S RETINA

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SUMMARY

1. Nine hundred and sixty cat retinal ganglion cells were evaluated with respect to receptive-field organization and latency to antidromic activation of their axons from optic-tract and mid-brain positions.

2. The vast majority (92 %) had the familiar concentric centre/surround organization. As in earlier work these could be classed as sustained or transient, independently of the centre type. About 13 % of the concentric cells were characterized by relatively sluggish responses to conventional visual stimuli which yielded brisk responses from the others. The sluggish cells constituted a previously unspecified class of concentric receptive fields.

3. The responses of brisk and sluggish cells to a variety of stimuli were described with a view to developing procedures for distinguishing them on functional grounds.

4. Measurements of latency to antidromic activation of retinal axons confirmed earlier work in showing that cells classed as brisk-transient had the shortest conduction times from the optic tract. Cells classed as brisk-sustained had intermediate conduction times and from earlier work would constitute an important input to the lateral geniculate nucleus. A proportion of the brisk-sustained axons reached the pretectal region (especially on-centre types) and a small minority reached the superior colliculus (especially off-centre types).

5. Sluggish cells had generally slower antidromic conduction times; despite some overlap with the brisk-sustained class, the slower conduction provided independent support for the functional differentiation. Sluggish axons reached the pretectal region and superior colliculus.

6. The brisk-sustained cells constituted the majority of the recordings in the *area centralis*.

7. A comparison with the morphological data of Boycott & Wässle is

made which suggests that the brisk-transient units corresponded with α cells, the brisk-sustained with β cells, and the sluggish units were included amongst the γ cells.

INTRODUCTION

In preceding papers (Cleland, Dubin & Levick, 1971; Cleland, Levick & Sanderson, 1973) an experimental basis for a classification of cat retinal ganglion cells has been developed. Various tests enabled a given cell to be recognized as either a sustained or a transient type. The classification was independent of the long-familiar on-centre/off-centre dichotomy described by Kuffler (1953), and thus four distinct categories of ganglion cells emerged: on-centre sustained, on-centre transient, off-centre sustained, off-centre transient. It was further shown (Cleland *et al.* 1971) that the sustained/transient classification was paralleled precisely by a dichotomous distribution of the time taken for an impulse to travel from the retinal ganglion cell to its synapse in the lateral geniculate nucleus: the axons of sustained cells conducted more slowly than those of transient cells, regardless of whether the cells were on-centre or off-centre. Thus the functional correlate of the two well-known conduction-groups in the cat optic nerve was shown to be the sustained/transient classification.

However, this is not the complete picture. The axons of retinal ganglion cells run not only to the lateral geniculate nucleus but also to the tectum, pretectal region and accessory optic nuclei (Barris, Ingram & Ranson, 1935; Laties & Sprague, 1966; Garey & Powell, 1968). Ganglion cells whose axons were confined to the latter destinations would not have yielded measurements of conduction time in the previous experiments (Cleland *et al.* 1971) and would not be represented in the dichotomous distributions of retinogeniculate latencies. In the present experiments, stimulating electrodes were placed on the central visual pathways so as to obtain latency measurements from all ganglion cells regardless of axonal destination.

Enroth-Cugell & Robson (1966) had already described a functional dichotomy of optic-tract axons in terms of linear/non-linear spatial summation ('X'/'Y' classification). When the sustained/transient classification was presented, the available data indicated that the equivalences: sustained = 'X' (linear), transient = 'Y' (non-linear) should be valid, though no checks of linearity were made. Independently, Fukada (1971) developed a classification employing the terms: 'type I' (phasic)/type II (tonic), on the basis of the time course of the responses to a long-lasting spot-stimulus (see Saito, Shimahara & Fukada, 1970). He related the functional classification to conduction velocity of the intracranial optic axons, but found substantial overlap in the respective distributions of

conduction velocity. Furthermore, Fukada encountered only *one* type II off-centre unit out of a sample of 336 axons sampled at the optic chiasm. Clearly, some caution is required in making the identifications: type I (phasic) = transient; type II (tonic) = sustained.

In the earlier work, we occasionally encountered concentric retinal ganglion cells having rather low responsiveness to manually controlled contrast targets and grating patterns. Although they could be classified as sustained or transient, the possibility of undetected inadvertent damage had to be kept in mind. In the present series of experiments we examined such occurrences in greater detail. It will be shown that such instances constituted a distinct subclass of concentrically organized ganglion cells. The present paper outlines the experimental basis for such a brisk/sluggish classification, which is independent of the sustained/transient and on-centre/off-centre classifications. Thus eight distinct categories of concentric units can be distinguished.

Since a large number of units was studied in the present series, the rarer classes of ganglion cells were also encountered in sufficient numbers for systematic study. These form the subject of the following paper.

METHODS

Experiments were performed on seventeen adult cats (2–4·5 kg). Anaesthesia was induced with 2–4 % halothane in a 2:1 mixture of nitrous oxide and carbogen and maintained for surgical procedures with 1–2 % halothane. Barbiturates were not used. The vagosympathetic trunk and carotid sheath were severed on the left side (for improved ocular stability) and a trachael cannula inserted. Penicillin ('Triplopen', Glaxo-Allenbury) was given I.M. in a dose of 200,000 u. daily.

Electrical stimulation. Shielded bipolar stimulating electrodes (1 mm bare tips, 1 mm tip-separation) were directed at the right superior colliculus and right optic tract. This necessitated alignment of the head in Horsley-Clarke stereotaxic planes and the provision of small craniotomy openings centred usually at anterior 3·0, right 2·0 and anterior 11·5, right 5·5 respectively (Reinoso-Suarez, 1961). Individual variations from cat to cat (Loewenfeld & Altman, 1956) automatically generated a range of effective stimulating sites. For the rear bipole the variation resulted in placements in both the tectum and pretectal region (Fig. 8 *C*, *E*). Conduction distances were checked after all experiments either by direct dissection of the fresh brain or by examination of a series of 1 mm-thick coronal sections of the formalin-perfused and fixed brain. Distances between stimulating sites and the junction of the optic nerve with the sclera of the left eye were directly estimated in every case by laying synthetic thread along the centre of the surface-visible pathway and measuring its length after straightening on a ruler. The mean distance to the optic-tract site was 24·7 mm, to the mid-brain site 53·1 mm.

Stimulus pulses, derived from an Ortec isolator (model 4656) and floating with respect to ground-reference, were coupled to the bipolar stimulating electrodes through a 0·47 μF capacitor; pulse durations were usually 50 μsec but were occasionally increased to 1 msec and amplitudes up to 80 V were used. An estimate of the electrode-pair impedance for a 50 μsec pulse was obtained by noting the change in

amplitude of the stimulus artifact when a 100 kΩ resistor was switched in series with the current path. This is not very accurate (because of possible stray electrostatic and inductive coupling between stimulating and recording circuits) but gave a result of 5–10 kΩ for electrodes in the brain. The lowest threshold for excitation of an axon in the optic tract was 220 mV, 50 μsec and for an axon in the superior colliculus 360 mV, 50 μsec. Wide, strong pulses were used sparingly. When this precaution was ignored, there was evidence of tissue damage around the electrode-tips: hardened cores of tissue with some dark staining.

Intraocular recording. Intraocular recordings (left eye) from ganglion cells and their axons were obtained with tungsten-in-glass electrodes (Levick, 1972) and glass micropipettes with tip-diameters less than 0·5 μm filled with 3·5 M-NaCl. In order to facilitate comparisons with the results of others, impedance measurements with alternating current at 50 Hz were made in Ringer solution: representative tungsten electrodes were in the range 30–200 MΩ; pipettes, 7·5–18 MΩ. With tungsten electrodes we find that the constructed shape is a more reliable predictor of performance. The amplified output was passed through a Krohn-Hite band-pass filter (Model 310C) with corner-frequencies set to 60 Hz and 6 kHz. Recording and display were conventional.

The corneae were protected with clear plastic contact lenses of zero power and atropine eye-drops (1 %) employed to dilate the pupil and paralyse accommodation. Neosynephrine (2·5 %) drops were used to retract lids and nictitating membrane on the left side. In all experiments the optic disk and the ophthalmoscopically estimated position of the *area centralis* were back projected on to a frontal tangent screen through the sight-hole of a firmly fixed hand-ophthalmoscope (Keeler) as described by Fernald & Chase (1971). The screen was located at a distance of 172 cm from the anterior nodal point of the left eye so that (ignoring tangent corrections) 1° of visual angle was subtended by 3 cm on the screen. During the experiment the exact centres of the receptive fields of all units studied were marked on the screen, together with symbolic identification. Calculations similar to those described by Bishop, Kozak & Vakkur (1962) were used to convert marked positions on the screen to azimuth and elevation relative to the presumed centre of the *area centralis* (system C co-ordinates). Some rolling of the left eye (torsion about its axis) was invariably associated with its fixation to the metal ring; therefore, the true position-angle of the optic-disk centre relative to the presumed *area centralis* and horizontal meridian was assumed to have the average value given by Vakkur, Bishop & Kozak (1963), namely $\psi B = 22{\cdot}2°$ (system E co-ordinates). Thus, an additional step in the calculations (a rotation about the line of sight through the projected *area centralis*) was required to obtain the final estimates of azimuth and elevation of every unit. The visual-field co-ordinates of all units studied are plotted in Fig. 1.

Procedure. Throughout the period of data collection the animal was maintained on a mixture of 70 % nitrous oxide, 28·5 % oxygen, 1·5 % carbon dioxide given by artificial ventilation at 33 strokes/min, with a stroke volume determined by the following formula: $S = 16{\cdot}6 \times W^{0{\cdot}77}$ where S is stroke volume in ml., W is weight of cat in kg. This was approximately *double* the volume given by the ventilation graph of the Harvard Apparatus Company (prepared by L. Kleinman and E. P. Radford). The percentage of nitrous oxide used has been shown to maintain a suitable level of light anaesthesia in cats (Venes, Collins & Taub, 1971). Muscular relaxation was obtained by I.V. infusion of gallamine triethiodide (Flaxedil) at 5 mg/kg.hr and D-tubocurarine at 0·3–0·5 mg/kg.hr. Tubocurarine was omitted during inactive stages of the experiments.

The recording electrode was first placed over the temporal half of the optic disk and the rear stimulating bipole advanced through the brain. As the expected level of the tectum was approached electrical stimuli (30–40 V at 50 μsec duration) were

applied at 1/sec and the threshold for the smallest detectable stimulus-locked deflexion of the optic-disk record noted. The threshold progressively fell with continued advance of the bipole as described by Granit (1955). Further advance was usually stopped when the threshold fell below 1 V. A similar procedure was adopted for placing the optic-tract bipole.

Since the optic pathway was rather dispersed at the level of the tectum and therefore difficult to stimulate in its entirety, advantage was taken of the topographic organization of the endings: each stimulus-electrode of the positioned tectal pair was used for recording a tectal 'swish' analogous to the geniculate 'swish' (Bishop,

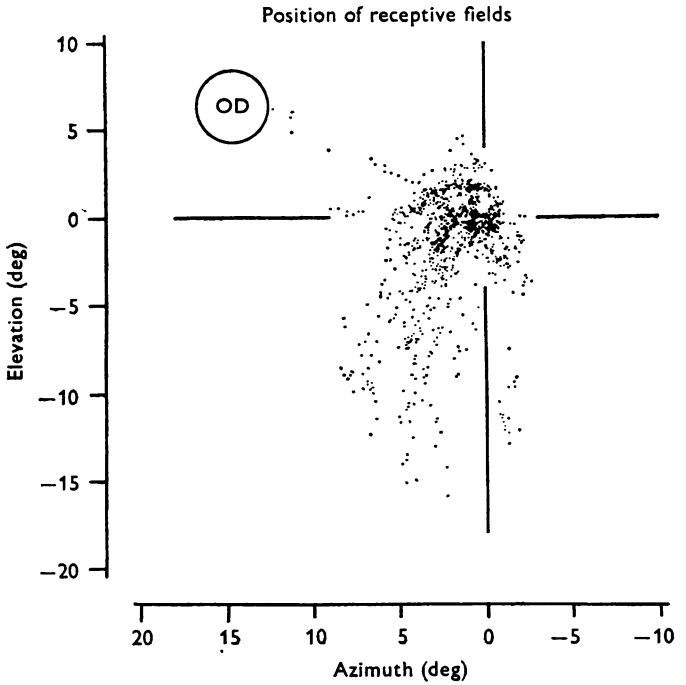

Fig. 1. Visual field co-ordinates of 960 retinal ganglion cells recorded in the left eye. Horizontal and vertical axes give the calculated azimuth and elevation relative to the estimated centre of the *area centralis* at the intersection of the indicated horizontal and vertical meridians. Conventions: positive, increasing azimuth corresponds to displacement to the left (temporal) of the vertical meridian in the visual field; positive, increasing elevation corresponds to displacement upward from the horizontal meridian. The circle (OD) represents an assumed approximate position (azimuth 14·6°, elevation 6·5°) of the optic disk.

Kozak, Levick & Vakkur, 1962) or cortical 'swish' (Cleland *et al.* 1971), elicited by oscillating hand-held targets to-and-fro in the proper part of the visual field of the left eye. The 'swish' was assumed to be the massed discharge of a large number of nearby post-synaptic units: it was frequently selective for the direction of target displacement and tended to habituate rapidly. The areas yielding 'swish' for each

electrode were outlined on the tangent screen and these zones became the target areas for recording ganglion cells in that experiment. The relative location of the pair of zones was generally consistent with the reported topographic representation on the tectum (Feldon, Feldon & Kruger, 1970). No 'swish' could be recorded when the electrodes were located in the pretectal region.

Visual stimulation. After the retinal electrode was relocated to the target zone, a round artificial pupil (area = 7 mm²) was placed immediately in front of the contact lens and a supplementary spectacle lens of appropriate power for the screen distance (172 cm) inserted in front of it. The correct power was determined by testing the responses of a briskly responding sustained unit to progressively finer grating patterns moved across its receptive field (Cleland *et al.* 1971) at the screen. Visual stimuli included black and white disks of various sizes mounted on thin wire handles and moved manually across the grey translucent surface of the fluorescent stimulator. Grating stimuli consisted of mounted photographic prints of parallel, equal width, black and white stripes producing a periodic square-wave profile of luminance (parallel grating). Two ranges of spatial frequencies were available: 0·5–8 c/deg, with a factor of $\sqrt{2}$ between steps; 0·94–15 c/deg, factor $=\sqrt[3]{2}$. 'Radial gratings' of similar construction were also used: each consisted of a circular area (angular subtense at the eye = 9°) divided into equal black and white sectors (sector angle usually 15°, ranged from 3·75 to 90°). Parallel gratings were moved perpendicular to the bars; radial gratings were rotated about the centre of the pattern. The approximate reflectances of the various surfaces were: white 0·9, black 0·1, grey 0·3. Stationary, flashed spots and annuli of controlled luminance and spectral composition were generated by a shuttered projector or the fluorescent stimulator (Levick & Zacks, 1970). These appeared as increments upon the background illumination produced by indirect, overhead, incandescent room lighting. Unless otherwise noted the grey background had a luminance of about 4 cd/m² (SEI photometer, Salford Electrical Instruments Ltd).

The receptive field of a unit was first sought on the tangent screen at 172 cm; contrast targets of various sizes were moved about until the region was found over which the maintained discharge could be strongly disturbed. A centre of symmetry was marked by making passes across the receptive field over a range of elevations and azimuths and also by applying centripetal and centrifugal movements in various directions. The size of the smallest disk having any effect and the size and speed producing an optimum response gave clues for the type of receptive field, as did the pattern of response to stationary targets and moving gratings of different spatial frequencies. For detailed investigation of receptive-field properties a mirror was interposed on the line of sight of the field so as to project it down upon the horizontal surface of the fluorescent stimulator at a distance of 57 cm from the eye. An additional +1·25 D lens was positioned in front of the eye for such work.

Centre sizes of receptive fields. Estimates were based on maps of the receptive fields (Hubel & Wiesel, 1962; Barlow, Hill & Levick, 1964) prepared by marking symbols at each position where a small exploring spot (about 20–100 × threshold at the very centre) was turned on and off. Each symbol indicated the presence and nature (on-excitation or off-excitation) of the response at that position. An estimate of the size of the receptive-field centre was made by drawing a continuous curve to encircle the places which gave the centre-type response (including the points giving both on- and off-responses). The curve passed midway between the outermost points giving the centre-type response and the innermost points for which no centre-type response occurred. The region so defined was usually circular, occasionally rather elliptical (e.g. Fig. 5*F*); therefore, an equivalent diameter was derived by calculating the geometric mean of the major and minor axes of the outline.

RESULTS

In seventeen adult cats, 1076 retinal ganglion cells and ninety-five retinal axons were examined in varying degrees of detail. A subset of 960 cells studied under uniform conditions of search and characterization constituted the reference sample for statistical purposes.

The investigation of each cell was begun by testing the responses to centripetal and centrifugal motion of manually controlled black and white contrasting disks. The initial aim was to decide if the cell was of the classical concentric type (Kuffler, 1952). Details of the testing are given in later sections; the result was that most (92 %) of the cells were of the concentric type. Those that were not are the subject of a separate paper (Cleland & Levick, 1974). The minimum information recorded on every unit in the sample included type of receptive field, visual-field position of its geometric centre, electrical thresholds and antidromic latencies for stimulation of the central visual pathway.

Units of all types were encountered with both tungsten-in-glass electrodes and electrolyte-filled micropipettes. Since there was no convincing evidence for differential selectivity between the two kinds, the data were pooled for the purposes of the present paper.

Subdivision of sustained and transient ganglion cells

In accordance with the previous work (Cleland *et al.* 1971) the application of a battery of tests (response to standing contrast, behaviour to grating patterns, sensitivity to size, speed and contrast of disk targets, presence of the periphery effect) enabled the concentrically organized ganglion cells to be classed as sustained or transient. However, the present extensive experience of ganglion cell performance revealed that the sustained and transient classes were not homogeneous. It emerged that about 13 % (113 out of 887) of the cells were distinguished by relatively sluggish responses to stimulation with moving targets (Fig. 2*B*, *E*) and also by a relatively low maintained discharge in the absence of such stimulation. The wave forms of sluggish cells often had a slower time course than those of the brisk cells (Fig. 2*C*). The different type of wave form and the low responsiveness to visual stimuli initially suggested the possibility of inadvertent damage. However, evidence to be presented elsewhere satisfied us that the recordings were not merely abnormal examples of the commoner briskly responding cells, observed under unfavourable circumstances; they constituted a distinct class of concentric receptive fields.

In the following sections some distinguishing characteristics of sluggish and brisk cells will be described. Only a start has been made along these

lines so far, since sluggish cells are relatively uncommon. Rather than develop an elaborate system of alphanumeric reference, the simple descriptive epithets 'brisk' and 'sluggish' will be used for the time being.

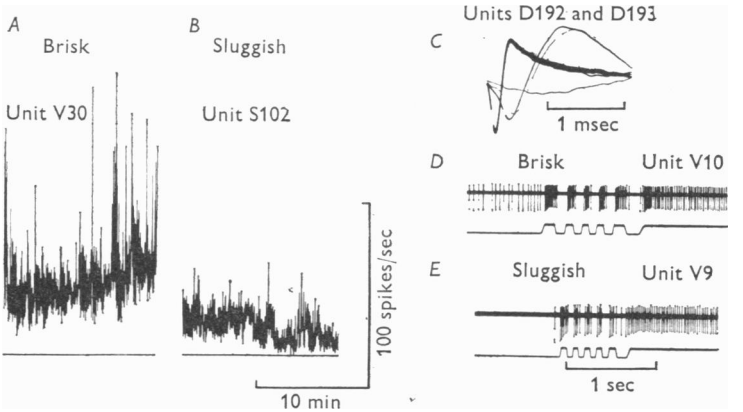

Fig. 2. Brisk and sluggish cells compared. *A*, *B*, sections of pen-recorder trace of mean discharge rate of representative brisk and sluggish cells during periods of comparable investigation with contrast targets and grating patterns. Base lines indicate zero frequency; time and rate calibrations are at centre, below. Throughout the period the discharge of the brisk cell reached substantially higher peaks than that of the sluggish cell, and the peaks were superimposed on a generally higher level of maintained discharge. *C*, spike wave forms of two simultaneously recorded cells (each about 0·5 mV, peak-to-peak). Triggering control was adjusted to cause oscilloscope time base to sweep whenever either spike occurred and multiple sweeps were photographed. The faster spike was that of an on-centre, brisk-transient cell and made a 'clacking' sound when reproduced on the audiomonitor. The slower spike (actually from a direction-selective cell) resembled in all respects that of a typical sluggish-concentric cell and it made a 'ploppy' sound on the audiomonitor. Short gaps in the initial descending phases of wave forms were produced by the blanking pulse from a Schmitt-trigger circuit for monitoring trigger levels. Conventions: downward deflexion indicates increasing positivity. *D*, *E*, responses to a grating pattern (1·4 c/deg). Upper trace of each record (*D*, on-centre brisk-sustained cell; *E*, on-centre sluggish-sustained cell, recorded consecutively in the same preparation) shows the spike discharge as the grating was moved briefly, then stopped. Lower trace of each record is the output of a photomultiplier directed at the region of the receptive field; a slit aperture oriented parallel to the bars of the grating was present in the intermediate image plane of an optical system in front of the photomultiplier. The bursts of impulses were more tightly packed in the case of the brisk cell.

Functional differentiation of the sluggish cells

Response to standing contrast. This was one of the principal tests for distinguishing sustained from transient cells, and it also provided some clues for separating sluggish from brisk cells within either category. The test was carried out by projecting a spot of light for on-centre cells or unmasking a black disk for off-centre cells (each upon the uniform grey background at 12 cd/m²) centred on the receptive field for 20 sec or longer. The response was monitored by displaying the mean impulse rate as a function of time on a chart recorder. Representative examples are shown in Fig. 3.

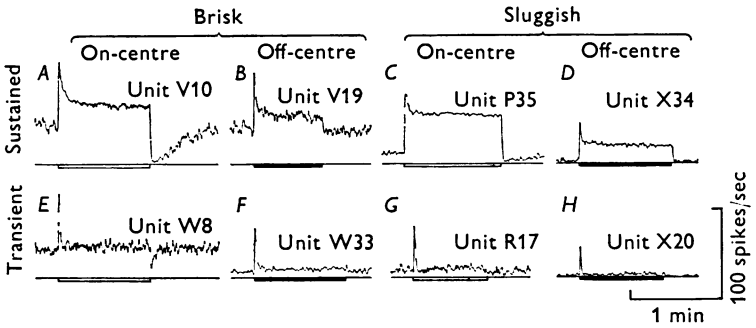

Fig. 3. Responses to standing contrast for all eight types of concentrically organized ganglion cells. A projected spot of light was turned on (*A*, *E*, *G*) or a contrasting disk was unmasked at the centre of the receptive field for the duration shown by the signal bar below each base line (□ brightening, ■ darkening); time calibration at lower right. Luminance of grey background was 4 cd/m²; reflectance of the grey, 0·3; of the white targets, 0·9; of the black targets, 0·1. The jagged line traces the mean discharge rate (calibration at lower right) derived from the impulse train by a smoothing circuit having an effective time constant of about 0·75 sec; the base line of each record corresponds to zero spikes/sec.

A, 0·5° spot, 10 cd/m²; *B*, 0·5° black disk; *C*, 0·8° white disk; *D*, 1·2° black disk; *E*, 1·0° spot, 6 cd/m²; *F*, 0·5° black disk; *G*, 0·5° spot, 20 cd/m²; *H*, 0·8° black disk.

From a moderately irregular level of maintained discharge, the response of the brisk-sustained on-centre cell rose sharply to a peak when the spot was turned on (Fig. 3*A*). Thereafter, the discharge declined first rapidly, then more slowly to a sustained plateau above the level of the pre-stimulus discharge. When the spot was turned off, the discharge ceased completely for a short while but then rose gradually to the pre-stimulus level. The behaviour of the sluggish-sustained on-centre cell (Fig. 3*C*) was rather different: the pre-stimulus maintained discharge was at a rather low level (12/sec) and relatively regular in pattern. At turn-on, the discharge

accelerated promptly and with minimal overshoot to a plateau which declined only slightly while the light remained on. The pattern of the discharge was remarkably regular as indicated by the narrow range of variation of the recorded trace. The maximum level of discharge did not much exceed that illustrated despite the use of stimuli with other sizes and intensities. As with most other sluggish-sustained on-centre cells, the strongest responses were obtained with spots of 1–2° diam., whereas the corresponding brisk cells required diameters of 0·3–0·7°. These dimensions apply to units recorded in the same retinal regions, within 15° of the *area centralis*.

Although the response illustrated in Fig. 3*C* could be considered representative of the sluggish-sustained on-centre class, a substantial range of variation was encountered. Some had a much more gradually increasing discharge at turn-on and others had no transient component at all. Although a low maintained discharge (4 cd/m^2 background) was common, some sluggish units did have rates up to 40/sec, but then the firing pattern was notably more regular than that of the brisk types.

Although a detailed evaluation was not carried out, at least 5 of the on-centre sluggish-sustained cells behaved like the 'luminance units' of Barlow & Levick (1969); in addition to the regular pattern of discharge and lack of crispness in the responses to wand stimulation, their equilibrium maintained discharge rate was a monotonically increasing function of background illumination over the range 0·034–50 cd/m^2 (the range usually tested).

When the standing contrast test was applied to off-centre sustained cells, it was not as easy to draw the distinction between brisk and sluggish types, since most of those considered to be sluggish had well developed leading transient phases preceding the plateau discharge (Fig. 3*D*). However, the low level of maintained discharge (about 1–5/sec, rarely more than 10/sec) and the relative regularity in the pattern of plateau discharge contrasted with the typical behaviour of the brisk units shown in Fig. 3*B*. It was again the case that the optimum targets for sluggish cells were distinctly larger (1–2° diam.) than those for brisk (0·3–0·7°).

No convincing distinctions could be drawn between sluggish and brisk cells of the transient class solely on the basis of the chart-recorded responses to standing contrast. The behaviour of typical representatives of each of the four varieties of transient cells is shown in Fig. 3*E–H*. The sluggish cells were diagnosed on the basis of other tests to be described. In all four examples, appearance of the target was followed by a rapid but short-lasting increase in firing which was succeeded by an irregular discharge not very different from the maintained discharge before stimulation. The discharge level during the presence of the stimulus was

a rather variable function of how far above threshold the particular target was.

One point of distinction tended to be masked by the limited band width of the chart-recorder: the burst of spikes from both of the brisk types (on-centre and off-centre) of transient cells was more tightly packed than that of the sluggish cells and produced a chirping sound on the audio-monitor. A further point was that the size of stimuli producing optimal responses was smaller for the sluggish cells (0·5–1°) than for the brisk (1–2°). This is the reverse of the corresponding relation for the sustained group.

Transient cells, brisk or sluggish, on-centre or off-centre, generally had an irregular pattern of maintained discharge.

Responses to moving targets. Closely associated with the description of ganglion cells as on-centre or off-centre types is the parallel description in terms of the responses to movement of contrasting stimuli. Thus Bishop *et al.* (1962*b*) referred to 'centrifugal-black' (or 'fugal-black') and 'centripetal-black' (or 'petal-black') responses, meaning that a unit gave increased firing as a small target darker than the background was moved respectively out from or into the centre of the receptive field. Centrifugal-black units were felt to be the on-centre type of Kuffler (1952) and the centripetal-black units were the off-centre types. It was found (for cat lateral geniculate neurones) that a centrifugal-black unit always gave centripetal-white responses, and correspondingly a centripetal-black unit always gave centrifugal-white responses. The same behaviour was also described and illustrated for concentrically organized ganglion cells of the rabbit's retina (Barlow *et al.* 1964).

In the present experiments the majority of concentric cells manifested the above type of behaviour; included in this majority were all the cells that were considered to be brisk on other grounds, plus almost half (twenty-two out of forty-nine surveyed) the cells similarly considered to be sluggish. For the remaining sluggish cells the response to centripetal movement of a target having the contrast appropriate for the centre of the receptive field was very much greater than the response to centrifugal movement of a target of opposite contrast. In an extreme case, for example the centripetal movement of a black disk on a grey background readily yielded excitatory responses, but no excitation at all could be produced by any movements of a white disk. In a number of such cases, it has been possible to obtain control observations against possible optical imperfections by virtue of simultaneous (but lower amplitude) recording of a typical brisk cell which gave symmetrical excitation to appropriately directed motion of targets of opposite contrast. In every case, the asymmetrically responding units were bracketed closely in retinal position between symmetrically responding brisk units, recorded in more or less close succession.

Some subtleties with the wand testing required special care. In the case of transient cells of either the brisk or sluggish type, it was possible to encounter misleading fugal/petal patterns if targets much smaller or much larger than the receptive field's centre were employed. The patterns arose in the following ways. When a 1° black disk was moved to the centre of the receptive field of an off-centre cell with a mapped centre of 2° diameter, there was an excitatory response corresponding to the centripetal motion. When the target was moved out, a further excitatory response occurred, so that one might have concluded that the behaviour was both petal-black and fugal-black. However, a test with partial movements revealed that the fugal-black response was attributable to the fact that the centrifugally moving target first encountered some of the uncovered central zone of the receptive field: it was clearly a 'centripetal' response for those particular parts of the central zone. Similar testing with a small white target showed that an unexpected petal-white response was attributable to passage of the target beyond that part of the central zone first encountered as the target made its way to the very centre.

A second source of misleading patterns was traced to the occurrence of responses from the surround. For example, when a large black target was moved away from the centre of an off-centre cell, an excitatory response was occasionally found. A test with partial movements revealed that the response actually appeared when the large black target moved off the on-surround of the cell near the end of the traverse. This was quite different in timing from the immediate response when a black target was moved away from the centre of an on-centre cell.

In most of the above cases, the behaviour could be simplified to the standard fugal/petal pattern by choosing a target of approximately the same size as the centre. This considerably strengthened the responses as well. The point made by these findings was that cells having receptive fields of the classical concentric kind could be induced to yield confusing responses by unfortunate choice of target size.

Speed of target motion. It was found that units considered to be sluggish on other grounds were primarily sensitive to slow movements (less than about 3°/sec) of appropriate targets. They continued to give significant perturbation of their low maintained discharge for target speeds up to about 30°/sec, but usually gave feeble responses when targets were flicked across the receptive field at about 100°/sec or faster. In contrast, the brisk-transient units always responded well at such speeds, and at least some of the brisk-sustained units also responded if the target contrast was appropriate to the centre of the receptive field (e.g. black target for an off-centre cell).

There was a particular refinement of the speed test that invariably separated the transient units into brisk and sluggish classes. It was applied as follows. A disk subtending 2° of visual angle had one surface black and the other side white; it was mounted at one edge on a coplanar handle of stiff wire by which it could be manually spun about its diameter. The spinning disk thus presented the black and white faces in rapid succession. This target was centred on the receptive field against a grey background and twirled at about 10–30 rev/sec. With the brisk type of transient unit (including both on-centre and off-centre types), it was always possible by a suitable combination of position and spin to drive the average discharge rate

steadily above 120 spikes/sec for at least a minute. The pulsating discharge made a characteristic chirruping sound on the audiomonitor. In the other class (sluggish) of transient unit, the average discharge rate could never be kept steadily above 75/sec; commonly it remained well below this level. A representative comparison of the two classes is shown in Fig. 4.

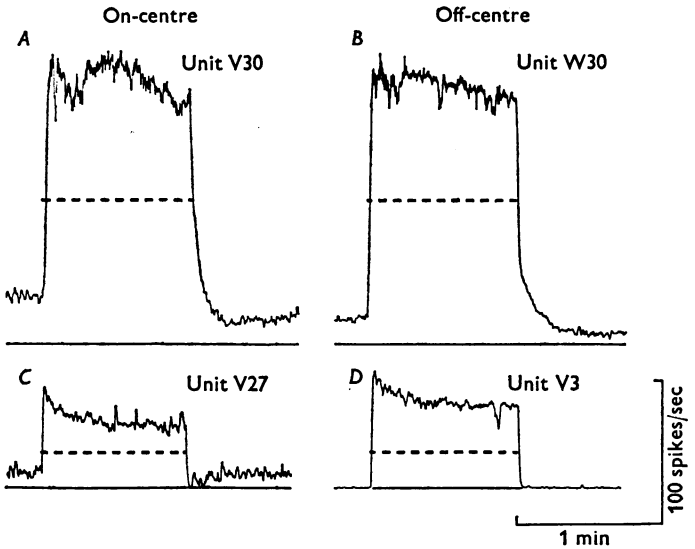

Fig. 4. Twirling stimulus test for distinguishing brisk-transient (*A*, *B*) from sluggish-transient (*C*, *D*) cells. Mean discharge rate of cells displayed as in Fig. 3. A disk subtending 1·3° and having opposite sides of black and white (reflectances: 0·1, 0·9) was rapidly spun over the receptive field centre (grey background reflectance: 0·3; luminance: 4 cd/m²) for the duration marked by the horizontal dashed line. The discharges of the brisk-transient (*A*, *B*) cells were driven well above 150/sec but those of the sluggish-transient cells (*C*, *D*), reached only 50–75/sec.

Receptive-field map. It was always possible to map out distinct centre and surround regions in the receptive fields of brisk cells by a proper choice of size and intensity of exploring spot. Typical maps of brisk-transient and brisk-sustained cells are shown in Fig. 5. It should be emphasized that the magnitude of responses was ignored in making the map. Surround responses to the exploring spot were always much weaker than centre responses.

It was not always possible to obtain correspondingly complete maps for sluggish cells. Particular difficulty arose with those off-centre types which behaved asymmetrically with respect to target contrast: they gave no excitation at all to a flashed spot of light and therefore lacked a receptive field in Hartline's (1938) sense. Nevertheless, at least part of the field could

be plotted with the help of a special stimulus: the idea was to produce a localized disk (0·3° diam.) of darkening to constitute the test-spot. It was achieved in two ways: (i) by projecting a spot of light on to an equal-sized disk of black card resting on the grey background; the intensity of the spot was adjusted to produce a match with the grey background when the light was on, and a spot of darkening appeared when the light went off,

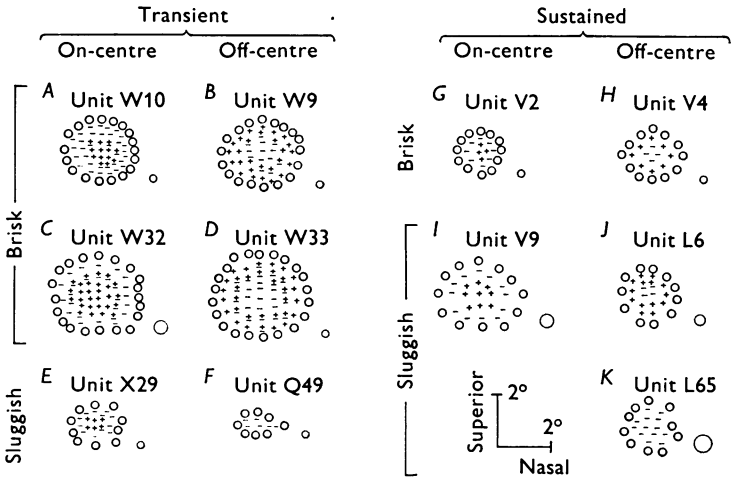

Fig. 5. Receptive-field maps of brisk and sluggish cells. Symbols: +, position of the test spot for which there was a response at turn-on; −, response at turn-off; ±, response at both turn-on and turn-off; ○, no response; there were no responses beyond the ring of ○'s. The extra circle near the lower right corner of each map indicates the size of the test spot; diameters (luminances): *A*, *B*, 0·25° (90 cd/m²); *C*, 0·5° (90); *D*, *E*, 0·25° (90); *F*, 0·25° (45); *G*, *H*, 0·25° (90); *I*, 0·5° (90); *J*, 0·4° (25); *K*, 0·6° (25). Luminance of uniform grey background was about 4 cd/m², except in *F* where it was about 15 cd/m² because of special arrangements (method (ii), see text). Scale and orientation for maps shown at bottom; apparent reversal of nasal and temporal directions attributed to use of mirror (see Methods).

(ii) a white card (reflectance 0·9) containing a small (0·3° diam.) aperture was centred upon the grey surface (reflectance 0·3) of the fluorescent stimulator; the luminance of the stimulator was adjusted so that the aperture matched the rest of the white card when the light was on. As before, a spot of darkening appeared when the light went off. Both methods were equally effective in eliciting excitation from those off-centre cells which failed to give off-responses to flashed spots of light. Receptive fields plotted with dimming stimuli were always small. In the example illustrated (Fig. 5*F*, method (ii)) the test spot was brighter than the background when on as well as darker than the background when off.

Apart from the above minority, the central zones of sluggish cells were readily plotted (Fig. 5*E*, *I*, *J*, *K*). Of the twenty-five maps available for detailed study, a clear-cut and complete surround was plottable in only six. In a further six, scattered patches of surround response were obtainable, but for the remainder there was no trace. Whether the surround was plottable or not, its response could almost invariably be revealed by the use of a concentric, annular stimulus with proper choice of the inner diameter. In the case of the transient variety of sluggish cells, it was often necessary to optimize the outer diameter of the annulus as well (see later).

Centre sizes. An estimate of the diameter of the region yielding centre-type responses was obtained from the receptive-field map (see Methods). The region included positions (if any) where on–off responses occurred. In Fig. 6*B* the centre sizes of sluggish units are plotted against eccentricity from the estimated position of the *area centralis*. Measurements from representative brisk-transient and brisk-sustained cells are included for comparison (Fig. 6*A*, *C*). It is apparent that the centres of sluggish units covered a wide range of diameters between the brisk-sustained cells below and the brisk-transient cells above, and overlapped both. Furthermore, there was no segregation of sluggish-sustained from sluggish-transient cells on the basis of centre size. A final point was that in all of the elongated receptive fields there was no evidence for a special selectivity to any particular orientation of edges or rectangular bars when tested with a variety of manually controlled targets.

Variation of properties with eccentricity. Fig. 6 shows that in the presence of some scatter there was an obvious increase in the centre size of the receptive fields of brisk-sustained and brisk-transient cells with increasing eccentricity from the *area centralis*, but there was no obvious gradient with the sluggish units. Furthermore, within the band representing the brisk-transient cells, the on-centre variety generally occupied the lower portion at each eccentricity with only occasional exceptions, i.e. within this class, on-centre cells had smaller centres than off-centre cells. There was a similar trend within the brisk-sustained class but it was largely masked by considerable overlap. No corresponding segregation could be discerned in the sluggish class.

In the case of brisk cells, there was a progressive decrease in the cut-off spatial frequency for moving square-wave gratings (highest spatial frequency reliably perturbing the maintained discharge) with increasing eccentricity which corresponded with the change in sizes of the receptive-field centres. Within about 1° of the centre of the *area centralis*, the cut-off spatial frequency was usually 5–6 c/deg, and at 12° eccentricity, it had decreased to 2–3 c/deg.

Again, in the case of brisk cells there was a definite impression that sustained behaviour was relatively enhanced at smaller eccentricities and transient behaviour at greater. Thus the standing contrast test with brisk-transient cells in the *area centralis* often revealed a small but definite sustained response in addition to the initial transient burst of impulses in

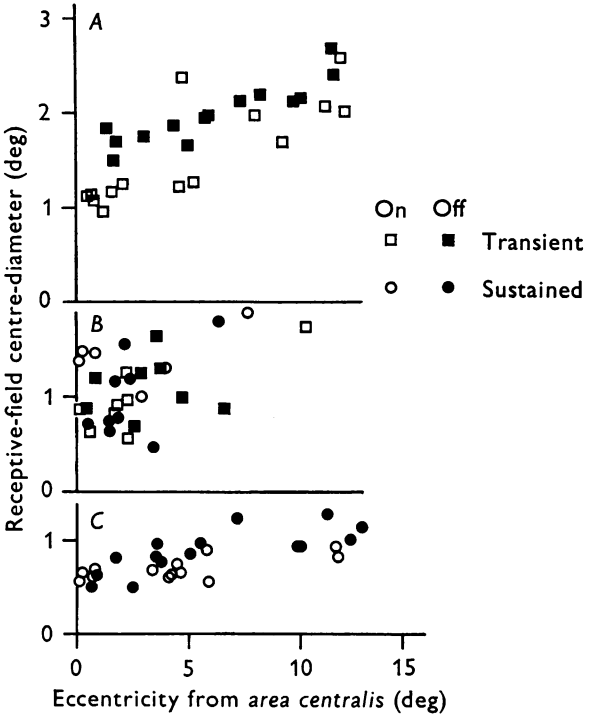

Fig. 6. Centre sizes as functions of eccentricity from the centre of the *area centralis*. *A*, brisk-transient cells; note the tendency for the on-centre variety (□) to have the smaller centre. *B*, sluggish-concentric cells; centre-size was unrelated to on-centre/off-centre or sustained/transient subdivisions (open/closed, circular/square symbols). *C*, brisk-sustained cells.

spite of careful adjustment of stimulus size. Similarly, brisk-sustained cells well away from the *area centralis* had a relatively more prominent initial transient burst in addition to the characteristic sustained component. The differential enhancement with eccentricity affected both sustained and transient cells equally, so that characteristic differences remained obvious at any particular eccentricity.

The vigour of responses also increased with eccentricity. For example application of the spinning disk test mentioned earlier to a brisk-transient cell in the *area centralis* usually did not lift the steady discharge rate

beyond about 120/sec, but when the test was applied to the same class of cell at say 10° eccentricity, a steady discharge of 175/sec was not unusual.

Finally, the periphery effect (see later) was relatively weakly represented in the *area centralis* but well developed outside it. Brisk-transient and brisk-sustained cells were similarly affected. With the former group the periphery effect was minor in the *area centralis* and strong outside; with the latter group it was absent in the *area centralis* and weak outside.

Tests with moving grating patterns. Brisk-sustained cells gave a response consisting of a modulation of their maintained discharge about the mean level for all grating periods down to the finest having a detectable effect. Brisk-transient cells gave a modulated response only to coarse gratings; this was replaced by an unmodulated increase in discharge during the passage of fine gratings or a brief augmentation of discharge when the finest detectable grating was jerked into motion.

No such distinctive patterns have emerged from the study of sluggish cells. The most common behaviour was a comparatively feeble modulated response which persisted to the finest grating causing detectable effects. This was observed whether the cell was sluggish-sustained or sluggish-transient. The cut-off spatial frequencies for different cells varied from 1 to 4 c/deg regardless of subclass (on-centre/off-centre; sustained/transient). It was quite uncommon to find the unmodulated type of response to fine gratings, but examples were encountered in all four subclasses. Eleven out of forty-three sluggish cells gave no response at all to gratings moved at the speeds which elicited optimum responses from brisk cells, i.e. 2–4 cycles passing a given point per second. However, it was found that when the passage frequency was reduced to 1 c/sec or slower, modulated responses appeared. In six out of the forty-three cells, there was evidence that the effect of gratings was *inhibitory*: for example, the maintained discharge ceased whenever a grating came to rest over the receptive field, although a modulated response was present during movement. In another case, stationary or moving coarse gratings stopped all discharge, although modulated responses appeared for fine gratings.

Silent inhibitory surround. During the conduct of grating tests, it was observed that the feeble response of sluggish cells could often be improved by restricting the amount of grating visible by interposing a grey screen in front of it having an opening 2–3° in diameter. By following up this observation it was found that the receptive fields of a substantial proportion of the sluggish units included an extra region in addition to the well recognized centre and antagonistic surround. This extra region appeared in uncomplicated form as a concentric annular area beyond the outer limit of the conventional surround component. Stimulation applied to this extra region had the effect of reducing or abolishing the excitatory responses produced

by simultaneous stimulation of either the centre component of the receptive field or the antagonistic surround component. For convenient reference in this paper, the inhibitory component will be called the 'silent inhibitory surround'.

The test for the silent inhibitory surround was constructed as follows. A 'radial grating' (see Methods) was arranged so that it could be manually rotated about its centre. The pattern was centred on the receptive field and an opaque grey disk was located centrally in front of it so as to hide the portions geometrically conjugate to the centre and surround components of

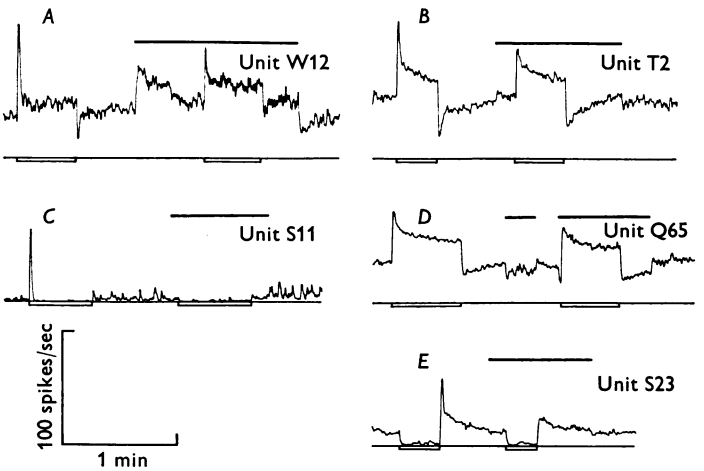

Fig. 7. Test for the silent inhibitory surround of brisk and sluggish cells. Two stimuli were applied to the receptive field in each case: (1) a projected spot (A: 1°, 2 cd/m²; B: 0·5°, 6 cd/m²; C: 0·5°, 20 cd/m²; D: 0·5°, 20 cd/m²; E: 0·5°, 20 cd/m²) on the centre, duration indicated by open bar under each base line (time calibration at lower left); (2) a radial grating (sector-angle 15°) obscured centrally by a grey disk (diameters – A: 3°, B: 3°, C: 2°, D: 3°, E: 3°) so as to confine the visible part to the region mainly beyond the conventional antagonistic surround. Each graph is mean discharge rate, as in Fig. 3, calibration at lower left. In each case, the spot was first turned on while the radial grating was stationary (control); the grating was then rotated about its centre for the duration indicated by the solid bar above and the spot again turned on during the rotation (test). A, brisk-transient and B, brisk-sustained cells: reduction of initial transient components of test responses (the concurrent excitatory effect of the grating on the maintained discharge in A is peculiar to the brisk-transient class (Cleland *et al.* 1973)). C, sluggish-transient cell: on-response completely abolished; D, sluggish-sustained on-centre cell: grating rotation caused sustained decrease of maintained discharge; a further application of grating rotation starting immediately before test spot caused only a slight relative reduction of response amplitude measured from the depressed level of maintained discharge. E, sluggish-sustained off-centre cell: transient component of off-response abolished.

the receptive field. The diameter of the disk routinely used subtended 3° at the eye, but other sizes were used as determined by the apparent size of the antagonistic surround. The control stimulus consisted of a spot or annulus projected on to the surface of the masking disk or a manually controlled contrast target moved to and fro over the surface of the disk. The existence of the silent inhibitory surround was tested by noting the effect on the control response when the radial grating was rotated.

Cells classed as brisk on other grounds had comparatively weak silent inhibitory surrounds as assessed by listening to the responses on the audio-monitor. When the responses were displayed on the mean-rate recorder, the effects of the silent inhibitory surround were rather more distinct (Fig. 7*A*, *B*) and consisted of a reduction of the transient components of the responses in both the sustained and transient types of cell. A detailed analysis of this will be presented elsewhere.

In the case of the brisk-transient class, there was a complication in that rotation of the radial grating on its own caused a continuing response (Fig. 7*A*) possibly originating from the antagonistic surround as suggested by Cleland *et al.* (1973). The qualification 'silent', while convenient for general application, will not be satisfactory for the brisk-transient class until the origin of the response and the nature of the interactions are better understood.

With thirty-five out of fifty-five sluggish cells the effects of the silent inhibitory surround were strong: a well suprathreshold excitatory response generated by stimulation of the centre or surround was completely eliminated when the radial grating was rotated at the same time (Fig. 7*C*, *E*). In a further six, the excitatory responses were greatly reduced. When the results were compiled according to the type of cell, it emerged that moderate or strong silent inhibitory surrounds were a feature of all sluggish varieties except for the on-centre sluggish-sustained subclass. In this group a silent inhibitory surround could not be demonstrated (Fig. 7*D*) in 11 out of 12 examples.

Incidental observations (on sluggish cells) yielded the following additional information. Stimulation of the silent inhibitory surround was observed to abolish the response to to-and-fro motion of a target across the receptive field; it could also slow or block the maintained discharge and reduce the discharge induced by electrode pressure. An attempt was made in five on-centre sluggish cells to assess the peripheral extent of the silent inhibitory surround by using progressively larger central masking disks. The inhibitory effects were found to fall off rapidly beyond 2·5° in four, beyond 2° in one. The spatial resolving power of the silent inhibitory surround was assessed on four on-centre sluggish cells by replacing the radial grating with conventional parallel gratings moved behind the masking disk. In three of the cells, inhibitory effects fell off sharply when the

spatial frequency was increased beyond 3 c/deg; with the other cell the limit was 2 c/deg. It was also noted that inhibitory effects could also be obtained when stationary flashing annuli were applied to the silent inhibitory surround. The inhibitory actions appeared both at 'on' and 'off' and were effective against excitatory responses elicited from the centre and conventional antagonistic surround (a small, limited annulus was used) provided that the excitatory and inhibitory stimuli were closely synchronized. Thus, the existence of a silent inhibitory surround was a factor responsible for previously mentioned difficulties in eliciting responses from the conventional antagonistic surround. It was found necessary in a number of instances to optimize the annular stimulus by reducing its outer diameter before convincing responses from the antagonistic surround could be revealed.

Finally, the comparison experiment has been encountered in which a a low-amplitude brisk cell was simultaneously recorded with a sluggish cell having a closely overlapping receptive field. It was noted that the responses of the brisk cell were relatively unaffected by stimulation of the silent inhibitory surround sufficient to block the responses of the sluggish cell completely.

Periphery effect. This has been described (McIlwain, 1964; Levick, Oyster & Davis, 1965) as an asynchronous augmentation of the maintained discharge to large-area visual stimulation applied well beyond (e.g. more than 20° away from) the conventional receptive field. The present experiments revealed that although the previous description (Cleland *et al.* 1971) was appropriate for brisk cells (i.e. periphery effect obvious with transient cells, absent or weak with sustained), there was little evidence of the periphery effect with sluggish cells whether sustained or transient.

Conduction times and conduction velocities

The placement of stimulating electrodes in the crossed visual pathway permitted measurement of the time taken for an antidromic impulse initiated in the axon at the site of stimulation to reach the retinal ganglion cell of origin.

In an attempt to establish comparable conditions for all axons, the electrical threshold was measured for the more sensitive direction of current flow through the stimulating bipole; the voltage was then increased to 1·4 times threshold for the latency measurement. Latency was measured from the beginning of the stimulus artifact to the beginning of the antidromically elicited action potential of the retinal ganglion cell, whether recorded as an initially positive-going or negative-going wave. The chance occurrence of an orthodromic impulse in the appropriate temporal vicinity of the stimulus artifact caused an all-or-none drop-out of the stimulus-locked wave form (by collision at some point along the axon) and thus provided not only a control on the antidromic nature of the stimulus-locked response, but also an

indication of any smaller, graded waves ('field potentials', Stone & Freeman, 1971) which might have confused the latency estimate. Since the 'field potentials' were always small or undetectable and the ganglion cell impulse was usually large there was no uncertainty in any of the measurements from this source.

Another infrèquent difficulty was related to the form of the antidromically elicited wave form. As described for other nuclear sites (motoneurones, Eccles, 1957; lateral geniculate neurones, Bishop, Burke & Davis, 1962), the antidromic wave form (when initially positive-going) always had a more sharply defined notch on its rising phase than the orthodromic wave form, and there were occasional examples when the component following the notch (B spike of Bishop *et al.* 1962*a*; SD spike of Eccles, 1957), appeared only intermittently or dropped out entirely in all-or-none fashion. Frequently this component showed substantial fluctuation in latency from trial to trial: longer latencies or complete drop-out were favoured if simultaneous visual stimulation was causing reduction in discharge; excitatory visual stimuli favoured increased occurrence of the B spike and shorter latency. Uncertainty in the latency measurements was therefore avoided by recognizing the above situation and restricting attention to the early component (A spike, IS spike) of the wave form.

It should be added that there were occasional instances (especially when the latency was long) where the complete wave form showed a fluctuation in latency of 2–3 msec at suprathreshold (1·4–2 ×) stimulus strengths. This could possibly be interpreted to indicate a special geometrical relation of the axon to the electrical field of the stimulus bipole (critical gradient reached at multiple points). The shortest latency was taken as the measure in such cases.

Antidromic activation from optic-tract stimulation

The distributions of latencies measured on 619 ganglion cells are shown in Fig. 8*A*, *B*. Examples of displays yielding the measurements are also shown (Fig. 8*G*, *H*). The positions of the receptive fields occurred over a region within 14° of the *area centralis*, including the latter. The frequency histogram for brisk units (Fig. 8*A*) had two clear modes and, with the exception of a single pair of units, these were non-overlapping. All of the cells in the short-latency group had been functionally assessed as transient type; all those in the longer-latency group were of the sustained type. There is remarkable general agreement between Fig. 8*A* and the histogram of retino-geniculate conduction times (Fig. 8 in Cleland *et al.* 1971) with regard to discreteness, spread and relative position of the distributions along the time axis.

The situation was quite different for the sluggish units (Fig. 8*B*): the latencies covered a substantial range and the mean (7·75 msec; S.D. = 3·24 msec) came at a much larger value than the means of the brisk-transient cells (1·63 msec; S.D. = 0·19 msec) or the brisk-sustained cells (3·58 msec; S.D. = 0·55 msec). Furthermore, there was considerable overlap of latencies for sluggish-transient and sluggish-sustained subclasses. Thus Fig. 8*A* may be taken to provide independent support for the brisk/sluggish functional distinction. However, the zone of overlap of the

histogram of Fig. 8*B* with the distribution of latencies of brisk-sustained cells shows that there would be a significant proportion of ambiguities were assessment to be based solely on measurement of latency.

There was no evidence that on-centre and off-centre cells had different latency distributions within any of the classes: brisk-sustained, brisk-transient or sluggish (*t* test).

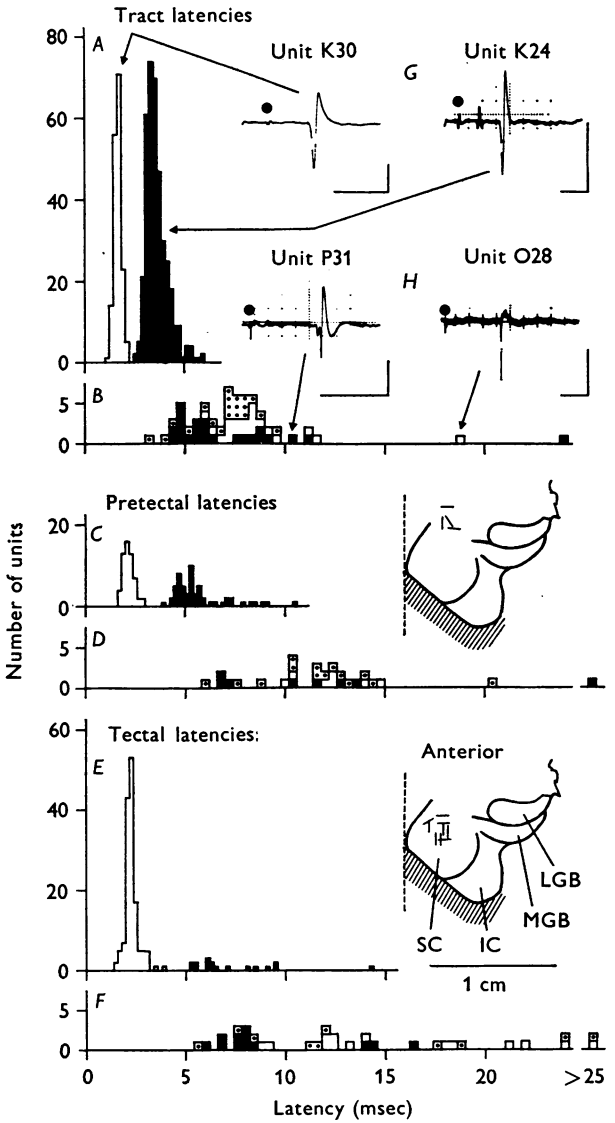

Fig. 8. For legend see opposite page.

Antidromic activation from pretectal stimulation. In four cats the rear bipole entered the dorsal surface of the brain-stem rostral to the superior colliculus. It was found that all varieties of both brisk and sluggish ganglion cells could be activated in varying proportions from this region. The frequency histograms of latencies (Fig. 8*C*, *D*) show features qualitatively similar to those of Fig. 8*A*, *B*: separated distributions for brisk-sustained and brisk-transient latencies (Fig. 8*C*); longer latencies for sluggish cells with substantial overlap of sustained and transient varieties (Fig. 8*D*); significant overlap of the histograms of sluggish cells and brisk-sustained cells.

When on-centre and off-centre cells were considered separately within each class, statistically significant departures from homogeneity emerged. In the brisk-sustained class, on-centre cells tended to have shorter latencies (mean 5·34 msec, S.D. = 1·16 msec, $n = 40$) than off-centre cells (mean = 6·39 msec, S.D. = 1·55 msec, $n = 17$; $P < 0{\cdot}01$, t test), whereas the relation was reversed for the brisk-transient class (on-centres: mean = 2·31, S.D. = 0·30, $n = 24$; off-centres: mean = 2·03, S.D. = 0·21, $n = 33$; $P < 0{\cdot}001$). There was no statistical evidence for differential regional sampling of the retina to account for the heterogeneity.

Antidromic activation from superior colliculus. The distributions of

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Legend to Fig. 8

Fig. 8. Frequency histograms of antidromic latencies following stimulation in optic tract, pretectal region and tectum. All histograms share a common abscissa scale (bottom). *A*, brisk-transient (□, $n = 171$) and brisk-sustained (■, $n = 383$) cells activated from optic tract. Oscilloscope displays which yielded measurements on typical examples are shown in *G* (conventions as in Fig. 2*C*); black dot near left end of each trace is centred over beginning of stimulus artifact. Calibration lines at lower right of each record: 2 msec and 1 mV. *B*, sluggish-concentric cells (conventions as in *A*; ⊡ indicates that sustained/transient property was not noted; insufficient observation) activated from optic tract (transient, twenty cells; sustained, twenty-four; not noted, twenty-one). Representative oscilloscope displays shown in *H*; calibrations: 10 msec and 0·5 mV. Unit P31 recorded with micropipette, all others with tungsten-in-glass electrodes. *C*, *D*, corresponding histograms for activation from pretectal region. The single, exceptionally long latency was 48·7 msec. Position and orientation of stimulating bipoles shown as short bars (connecting electrode tips) on the tracing (left) of the upper end of the brain stem in plan view (mid line shown dashed; anterior is towards the top). The tracing was made from a photograph from above of the stereotaxically oriented structures exposed by dissection. Cross-hatched region is the bony tentorium overlapping superior colliculus (SC in *E*) and inferior colliculus (IC); MGB, LGB: medial and lateral geniculate bodies. Calibration below. *E*, *F*, corresponding data for activation from tectal stimulating sites. The two exceptionally long latencies were 28·7 and 35·9 msec.

latencies for brisk and sluggish ganglion cells are shown in Fig. 8*E*, *F*. There was a great reduction in the number of brisk-sustained cells, particularly the on-centre type, which could be activated from this site. Otherwise, the histograms reflect the properties already described. The corresponding tests for heterogeneity were inconclusive for the brisk-sustained class, but reflected the previous tendency in the brisk-transient class (on-centres: mean = 2·35 msec, S.D. = 0·44 msec, $n = 60$; off-centres: mean = 2·22 msec; S.D. = 0·22 msec, $n = 84$; $P < 0{\cdot}01$).

Heterogeneity due to visual-field position. This potentially important factor affecting the spread of the distributions of conduction times was assessed by plotting scatter diagrams of conduction times from the various central sites against angular eccentricity from the optic disk. The example (Fig. 9*A*) is for the optic tract site and it includes all of the electrically excitable brisk and sluggish units recorded at the cell body site in the retina. The first point to be made is that there was a positive gradient of conduction time *vs.* eccentricity from the disk which was most obvious for the brisk-transient cells (all the dots below 2·5 msec) and still quite definite (correlation coefficient = 0·273; Fisher's z test: $P < 0{\cdot}001$) for the brisk-sustained cells (all the dots above 2·5 msec). No trend was evident with the sluggish cells (+).

The second point is that there was a local upward spread of conduction times at eccentricities (14–16°, Vakkur *et al.* 1963) corresponding to the position of the *area centralis*; it was most obvious for the brisk-sustained cells and was suggested by four brisk-transient cells with latencies longer than expected. A review of the data confirmed that all types of brisk cells had rather longer latencies at and near the *area centralis*. A detailed analysis will be presented elsewhere, but it may be stated here that the results gave no support for the proposal (Stone, Freeman & Holländer, 1971; Stone & Freeman, 1971) that there were two additional discrete, conduction velocity groups arising from the *area centralis*. The latencies of both types of brisk cells decreased *continuously* with distance from the *area centralis* in all directions and with substantial scatter, to merge with the general pattern of latencies for the non-central retina.

The final point is that Fig. 9*A* confirms the essential separateness of the brisk-transient and brisk-sustained cells with respect to conduction time. Additionally it gives a clearer picture of the extent of overlap between the sluggish and the brisk-sustained cells. A careful review of the detailed protocols of cells in the range of overlap gave no cause to reclassify them except in the case of the sluggish cell having a latency from the optic tract of 3·08 msec: it had not been held for long and might possibly have been an example of a damaged, brisk-sustained type. It is not included in the range of overlap indicated by the dotted bracket.

The corresponding scatter diagrams for the pretectal and tectal stimulating sites revealed patterns similar to those of Fig. 9*A*.

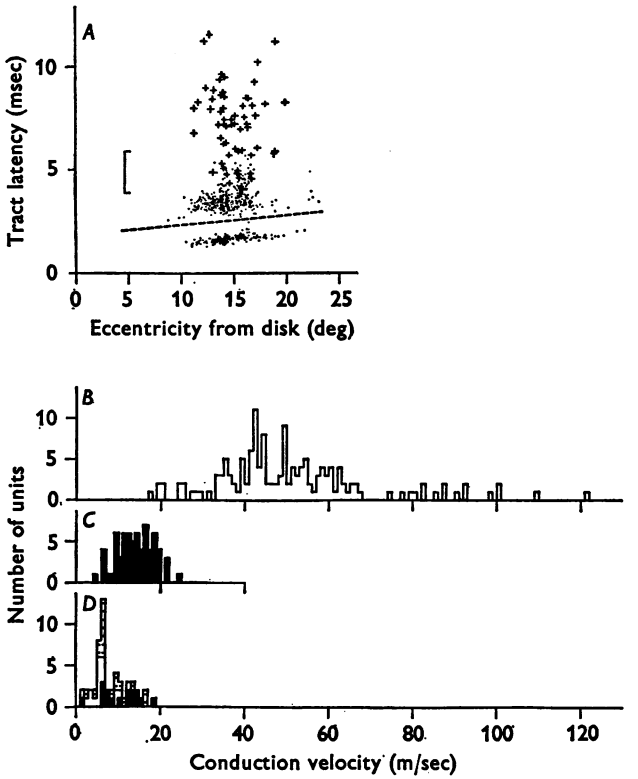

Fig. 9. *A*, scatter diagram of antidromic latency with optic tract stimulus (vertical axis) against eccentricity of receptive field centre from optic disk. Brisk-transient cells (171) shown by fine dots below the sloping dashed line, brisk-sustained cells (383) by fine dots above the line, sluggish cells (65) by + 's. The dotted vertical bracket encloses a region of overlap between the latencies of brisk-sustained and sluggish cells. The overlap involved cells having receptive fields in the same retinal regions. *B*, *C*, *D*, frequency histograms of the conduction velocities of brisk-transient, brisk-sustained and sluggish-concentric cells, respectively. *Key*: □, transient; ■, sustained. In *D*, cells for which the sustained/transient property was not noted are indicated by dotted blocks (⊡). The distributions overlap to various extents.

Conduction velocities. Since substantial numbers of brisk and sluggish ganglion cells could be electrically activated from both the optic tract and mid-brain sites, it was possible to obtain estimates of conduction velocity

between those sites from the measured conduction time differences and conduction distance. Histograms of conduction velocities of 275 ganglion cells are shown in Fig. 9*B–D*. Perhaps the most significant fact is that ganglion cells having the familiar concentrically organized receptive fields ('Kuffler-type' units) did have conduction velocities covering the entire range from 1·1 to 120 m/sec. The fastest-conducting fibres belonged to cells of the brisk-transient class and they formed a group (Fig. 9*B*) which was largely distinct from the remainder (mean = 51·9 m/sec; S.D. = 18·4; n = 154). The existence of overlap in the range 17–25 m/sec is worth noting. The sample for this illustration was a subset of that used to generate the latency histogram of Fig. 8*A* which demonstrated separated distributions for brisk-transient and brisk-sustained classes. Therefore, representing the data in terms of conduction velocity actually caused some blurring of an otherwise sharp separation.

The slowest conducting fibres belonged to ganglion cells of the sluggish class (Fig. 9*D*). Within this histogram the on-centre sluggish-sustained cells tended to predominate in the slow velocity (left-hand) end and the off-centre sluggish-sustained in the higher velocity end, while the other two subclasses were intermediate. Since overlap was extensive, any suggestion of grouping in terms of conduction velocity could be easily refuted by relatively numerous exceptions from the data. A further point is that there was substantial overlap of the distribution of the sluggish cells (mean = 8·3 m/sec; S.D. = 4·1; n = 53) with that of the brisk-sustained (Fig. 9*C*; mean = 14·1 m/sec; S.D. = 4·25; n = 68).

We considered the possibility that the brisk-sustained cells of Fig. 9*C* represented a small and special subset of the sample by virtue of their mid-brain destination; for example, the conduction velocity distribution for the axons not destined for the mid-brain (presumably the majority) may have been much narrower. Therefore, separate distributions of the latencies to optic-tract stimulation were compiled for the brisk-sustained cells classified according to whether they could or could not be antidromically activated from the mid-brain. For the pooled on-centre and off-centre data the results were as follows. Cells activated from the mid-brain: mean = 3·50 msec, S.D. = 0·77 msec, sample size = 68; not activated from the mid-brain: mean = 3·61 msec, S.D. = 0·49 msec, sample size = 308. There is little difference in the means but a statistically significant difference in spread (variance ratio test, $P < 0{\cdot}01$), which was shown by further analysis to be attributable to faster conducting on-centre axons and slower conducting off-centre axons in the mid-brain activated sample. The difference in spreads was not very great and would not alter the conclusion from Fig. 9*C*, *D* that there was substantial overlap in the distributions of intracranial conduction velocities of brisk-sustained and sluggish axons.

Electrical thresholds

Under uniform conditions it has been found that the threshold for brief electrical stimulation is inversely related to diameter of the axon stimulated (Erlanger & Gasser, 1937; Bishop, Clare & Landau, 1969). We therefore examined measurements of threshold in relation to the different functional classes of concentrically organized retinal ganglion cells.

The first point to emerge was that electrical thresholds for antidromic activation were widely scattered (from a minimum of 0·21 V at 50 μsec to 80 V at 100 μsec, at the optic tract site) for both brisk and sluggish cells. There was no exclusive range for a particular class.

It should be mentioned that for arithmetical purposes a voltage threshold at twice the normal pulse duration was taken to be equivalent to twice the voltage at the normal duration (50 μsec). Since non-standard durations were rarely used and since specimen strength–duration curves demonstrated reciprocity over this range of duration, no significant error would be expected.

Statistically significant differences (t test) did appear when mean thresholds for the different classes were compared. At all stimulating sites, brisk-transient axons as a class were more sensitive than brisk-sustained or sluggish, but it was only at the optic tract site that brisk-sustained axons were significantly more sensitive than sluggish. Within the various classes, on-centre and off-centre populations were statistically indistinguishable except at the tectal site for brisk-transient axons (off-centres more sensitive) and at the optic tract site for sluggish axons (on-centres more sensitive). In absolute terms, all classes of axons were more sensitive at the optic tract site than elsewhere.

Some of the individual scatter was undoubtedly caused by observed variation in the relative position of stimulating electrodes. Nevertheless, there were a number of examples in any given preparation of wide variations of threshold in a given class of cell despite close proximity of receptive-field positions and temporal proximity of the recordings. There were also many examples where the relative sensitivity of members of the different classes was in the opposite sense to the means of those classes.

Retinal distribution

The distinctions brought out in previous sections made it possible to devise a reliable procedure for functionally classifying any particular ganglion cell (see Discussion). The complete picture would necessarily include some relatively rare classes which are the subject of the following paper (Cleland & Levick, 1974); a full table will be presented there.

In a sample of 960 units encountered as cell body recordings, 887 (92 %) were of the concentric type dealt with in this paper; 774 (80 %) were classed as brisk, 113 (12 %) as sluggish. The brisk cells comprised 243 transient

type (25 %) and 531 sustained type (55 %), while the sluggish group were made up of twenty-seven which were transient, forty-four which were sustained and forty-two for which the sustained/transient property was not determined because of insufficient examination (recorded early in the series). Within each class, on-centre and off-centre cells were equally frequent, to within the limits of sampling variation.

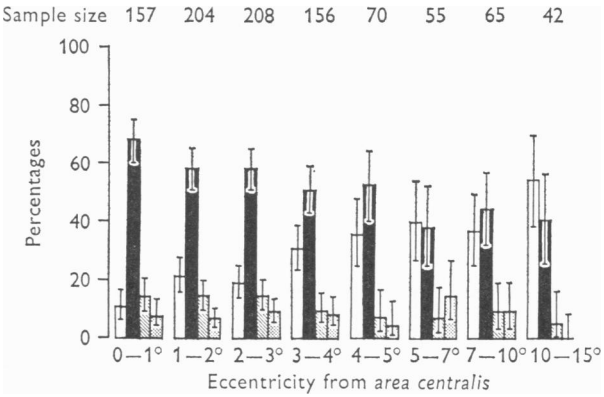

Fig. 10. Percentage distribution of ganglion cells by receptive-field class at various eccentricities from the centre of the *area centralis*. The vertical lines at the top of each block give the 95 % confidence band for the estimate of the population percentage. The three undiagnosed cells in the reference sample of 960 have been excluded. 'Other types' of receptive fields (seventy) are dealt with in the following paper. The remainder constitute the classical concentric type. *Key:* □, brisk-transient; ■, brisk-sustained; ▨, sluggish; ▦, other types.

Cells of all subclasses of both brisk and sluggish types were encountered in all retinal regions explored (see Fig. 1 for coverage). However, the relative frequencies varied systematically with eccentricity from the presumed *area centralis* (Fig. 10). It is important for the interpretation of percentages to state the way in which exploration was performed. Over the region within about 4° of the centre, we proceeded along a straight or gently curving traverse across the retina in very small steps (approximately 15 μm on the retina), attempting to record from every ganglion cell on the path. To indicate how this procedure might yield different results from a 'random' search, it was observed that the same brisk-transient cell was often re-recorded on two to three successive placements, a brisk-sustained cell was occasionally re-recorded on two successive placements and a sluggish cell was very rarely recorded more than once. The re-recording of a cell was recognized by observing identity of receptive field type and position together with close agreement of electrical thresholds and latencies for antidromic activation. Naturally, re-recordings of the same cell were

not added to the sample. At greater eccentricities than about 5°, the above procedure was too slow because of the rising proportion of unfruitful placements (lower ganglion cell density). We then took larger steps and reverted to small steps only when necessary to improve the recording of a spike within the noise level.

In confirmation of earlier work (Cleland *et al.* 1973) it was found that brisk-sustained cells were encountered much more frequently than brisk-transient at the presumed *area centralis*; the proportion was progressively reduced with increasing eccentricity to reach approximate equality beyond 10°. The relative proportion of sluggish cells reached 14% within 1° of the centre and it progressively fell with increasing eccentricity. The limited sample sizes preclude a stronger statement.

DISCUSSION

Differentiation of concentric receptive fields

On the basis of the preceding results, it became possible to define guide lines for classifying ganglion cells physiologically. It is important to discuss the procedures in order to convey a proper impression of the appropriateness of the subdivision and the reliability of the tests. In general, it was necessary to take the results of all the tests in conjunction to arrive at a reliable diagnosis, since there were significant regions of ambiguity with any one particular test.

Brisk-transient cells constituted the most distinct subdivision of the classical concentric units. Members of this group responded optimally to targets of 2° diameter or larger and gave vigorous bursts making a characteristic sound on the audiomonitor when large targets of either contrast were flicked rapidly across the receptive field. They were also the only class of cell which could be driven to mean discharge rates of over 120/sec continuously by the twirling stimulus test (Fig. 4), and they usually yielded an easily elicited and prominent periphery effect. Fine gratings moved across the receptive field caused an unmodulated increase in the discharge rate. The functional testing rarely left any doubts and absolute confirmation was provided by the electrical tests: brisk-transient cells were readily activated from tectum, pretectum and optic tract, and the antidromic latency from the latter site was always shorter than that of any other class at a given eccentricity from the optic disk.

Brisk-sustained cells formed the next most distinct group. A strong, irregular maintained discharge ($\sim$40/sec) was usually present. A small pupil and correct focusing (see Methods) were important for characteristic behaviour. Cells in this class often gave distinct responses to contrast

targets only 10 min arc in diameter; the moving target yielding an optimal response was obviously smaller than with brisk-transient cells in the same general region. The characteristic modulated response to fine grating patterns was rarely approached with other classes of cells. The latency pattern was often distinctive: antidromic activation from only the optic tract site with a latency of 3–4 msec.

In the functional differentiation it was important to keep in mind the controlling influence of eccentricity from the *area centralis* upon the various properties. For example, Fig. 6 shows that the size of the centre zone of a brisk-transient cell close to the *area centralis* could be smaller than that of brisk-sustained cell at 11·5° of eccentricity. To the extent that the results of differentiating tests applied depended upon the centre size, the parameters of those tests had to be properly chosen in relation to the eccentricity of the cell from the *area centralis*. This point was particularly relevant to the tests with standing contrast, target size and gratings (page 435).

Sluggish-transient and sluggish-sustained cells did not form such compact groups as their brisk counterparts because of a substantial range of individual variation. It would therefore be rather misleading to describe as 'typical' any particular examples of the transient and sustained varieties. In practice, a sluggish type was suspected if a concentric unit failed to meet some of the test specifications for brisk-transient and brisk-sustained types under recording circumstances where retinal image quality was good, the preparation was healthy, and significant damage seemed unlikely. Features which quickly drew attention were: (1) low maintained discharge; (2) low responsiveness (but not necessarily low sensitivity) to stationary or moving visual stimuli; (3) unusually regular discharge during the standing contrast test (sustained types); (4) lack of responsiveness of an off-centre unit to centrifugal white targets or of an on-centre unit to centrifugal black targets; (5) with moving gratings, a special requirement for low bar-passage frequency and/or prominent inhibitory effects; (6) demonstration of a strong silent inhibitory surround; (7) map of receptive field with poorly represented surround responses; (8) antidromic latency from the optic tract site in excess of 6 msec; (9) antidromic activation possible from the tectal stimulus site.

Not all of the features were possessed by all of the sluggish units; nor were all of the features confined exclusively to them. For example, not all sluggish units had low maintained discharge; some of the brisk units (particularly within the off-centre brisk-transient subdivision) did have low maintained discharge. A significant proportion of sluggish units had antidromic latencies from the optic tract site shorter than 6 msec and overlapped in this respect members of the brisk-sustained class with receptive fields in the same retinal region (Fig. 9*A*).

'X-cells' and 'Y-cells'

The X/Y classification introduced by Enroth-Cugell & Robson (1966) was based on observations establishing that summation over the receptive field of X cells was approximately linear, whereas for Y cells it was very non-linear. The brisk-transient and brisk-sustained cells of the present paper are presumably Y cells and X cells respectively. It is not known if the sample of Enroth-Cugell & Robson included sluggish-concentric cells; nor have we specifically determined which members of the sluggish class were linear or non-linear.

Relation to anatomy

Boycott & Wässle (1974) have shown on morphological grounds that cat retinal ganglion cells may be classified into at least three types: α, β and γ. The first two constitute more homogeneous groups than the third, which might eventually be shown to comprise distinctive subgroups. One of the key simplifying insights to emerge was the demonstration of a systematic variation of dendritic field size and to some extent cell body size, and qualitative variations in appearance as functions of eccentricity from the *area centralis* within the groups α and β. With the advent of the new morphological data and the physiological information of the present paper, the argument begun in Cleland *et al.* (1973) relating structure and function may now be continued.

The brisk-transient and brisk-sustained classes constituted two distinct, compact groups from the point of view of functional testing. In each case the sizes of the receptive field centres covered relatively small ranges respectively at a given eccentricity and the sizes were systematically graded with eccentricity from the *area centralis*. The respective latencies for antidromic activation also formed distinct, compact distributions. On the other hand, the remainder of the ganglion cells (sluggish concentric types of this paper plus the rarer classes of the following paper), if considered as a third 'group', covered a wide range of physiological performances; the sizes of their receptive field centres covered a wide range, overlapping the first two classes, and without obvious gradation with eccentricity. The antidromic latencies were also widely scattered.

Thus it is natural to consider the identification of the two kinds of brisk units with α and β cells and the remainder with the γ cells. Relative frequencies of occurrence and retinal spacing are of no assistance because the caprice of Golgi-staining invalidates comparison with morphological frequencies. However, there are two other aspects which give important clues.

Dendritic trees and receptive fields. Over the first 12° of eccentricity from the *area centralis*, the brisk-sustained units had smaller receptive field

centres than the brisk-transient units and are therefore the candidates for identification with the β cells, the elements having the smallest dendritic spreads. In Fig. 11*A*, the centre diameters have been plotted together with the dendritic field diameters of the β cells abstracted from the data of Boycott & Wässle (1974). The centres are substantially greater but increase in parallel with the dendritic fields as eccentricity increases. There is rather more absolute variation in centre sizes than in dendritic fields.

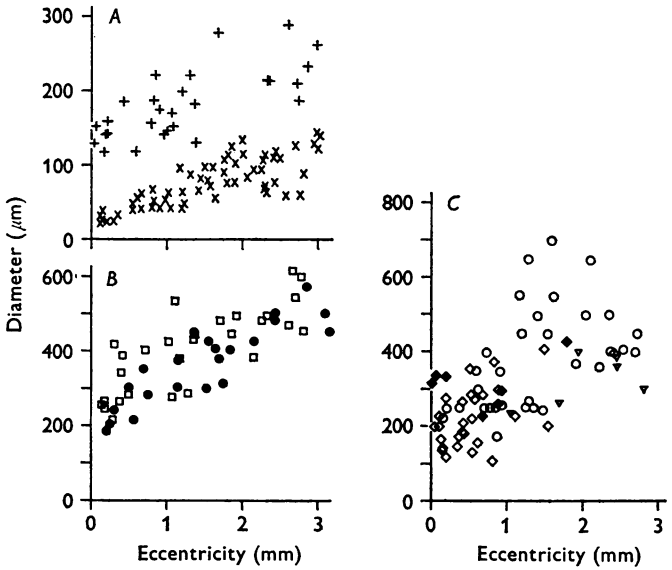

Fig. 11. Comparison of receptive field centre sizes with dendritic fields as functions of eccentricity from the *area centralis*. *A*, Brisk-sustained centres (+) and dendritic fields of β cells (×). *B*, brisk-transient (□) and α cells (●). *C*, sluggish (◇, ◆) and γ cells (○, ▽); ◆ signifies members of the subclass: on-centre sustained; ▽ signifies members of the δ subclass. The physiological parameters were converted from angular measure to retinal distance on the assumption that 1 mm on the retina subtended 4·4° in the visual field. Note the expanded vertical scale in *A*. Dendritic fields replotted from Boycott & Wässle (1974).

A similar comparison of brisk-transient centre sizes and α-type dendritic fields (Fig. 11*B*) reveals rather remarkable congruence of the two measures at all eccentricities. The two measures also show similar patterns of spread with eccentricity.

The comparison between γ-type dendritic fields and centre sizes of the pooled sample of sluggish concentric units (Fig. 11*C*) is hampered somewhat by disparate proportions of data at different eccentricities. Nevertheless, there is considerable overlap of the respective distributions at various eccentricities. On the whole, the centres are smaller than the den-

dritic trees. Special properties of some of the receptive fields (requirement for dimming stimuli for mapping; presence of a strong silent inhibitory surround) may have tended to produce smaller mapped centres.

One of the main difficulties in a comparison of centre sizes and dendritic fields of different classes of cells is the rather arbitrary nature of the specification of receptive field centre size. Various measures have been used. In this paper, centre size is derived from the area over which a centre-type response can be obtained (as in mapping the receptive field). Cleland *et al.* (1973) used the diameter of an equivalent idealized centre mechanism with a rectangular sensitivity profile having the same threshold for a small spot and the same minimum threshold (Cleland & Enroth-Cugell, 1968). Enroth-Cugell & Robson (1966) assumed idealized centre- and surround-mechanisms having sensitivity profiles of Gaussian shape; for comparison with diameters of dendritic trees they used a value of 5 times the standard deviation of the Gaussian profile for the centre mechanism. Wiesel (1960) used the diameter of the spot for which the incremental threshold (*vs.* diameter) was at its minimum value. Each of these conventions (and others like them) has implicit assumptions about the physiological mechanisms underlying the organization of the receptive field. In view of the physiological diversity, it may well be that a convention appropriate for one class of ganglion cells would be inappropriate for the others. Any qualitatively differential behaviour between the classes with respect to the parameters of a particular measuring technique (e.g. background illumination, intensity and size of a test spot) may generate systematic shifts in the actual numbers obtained.

It is perhaps asking too much to expect universal numerical congruence between consistently derived physiological and morphological measures. The thrust of our argument therefore lies less in the precise matching of numbers than in the correspondences which exist when the physiological and morphological groups are (1) placed in order of size, and (2) considered in terms of intrinsic variation and variation with eccentricity.

Axonal size. A second significant point of contact between the morphology and physiology concerns the axons of the different classes. Although they had to assess the diameters of the axons subjectively, Boycott & Wässle (1974) found that at equivalent retinal points the axons of α cells were larger than those of β cells which were in turn larger than those of γ cells. These facts fit in well with the proposed identifications because over the limited range of eccentricity studied the axons of the brisk-transient cells had (*a*) the shortest conduction times from particular central stimulus sites, (*b*) the fastest conduction velocities between central stimulus sites and (*c*) the lowest electrical thresholds, on average, at central stimulus sites; all of these points suggest the largest axons. Although there was

some overlap in the case of brisk-sustained and sluggish cells, the corresponding considerations suggest that brisk-sustained axons are in turn larger on average than sluggish axons.

Boycott & Wässle also stated that the diameters of the axons of α and β cells increased proportionately with increasing distance from the central area. This also fits in with our physiological observations: (*a*) there was for both brisk-transient and brisk-sustained types a local progressive increase in antidromic conduction time for cells near the centre of the *area centralis* as compared with neighbours on three sides; (*b*) there were occasional instances of multiple unit-recordings in which one element was a brisk-transient cell and the other was a fibre of passage from a more peripheral brisk-transient cell within the same hemiretina. Invariably, the antidromic latency from the optic tract site was shorter (i.e. faster conduction 'velocity') for the fibre of passage. To what extent these observations indicate eccentricity from the *area centralis* or from the optic disk as the controlling parameter will be taken up separately.

Conclusion

The combination of anatomical and physiological data provide reasonable grounds for the following correspondences: α cells with brisk-transient cells; β cells with brisk-sustained cells; γ cells with sluggish-concentric cells. It will be argued in the following paper that the ganglion cells lacking the familiar concentric receptive fields also corresponded with γ cells.

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