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SUSTAINED AND TRANSIENT NEURONES IN THE CAT'S RETINA AND LATERAL GENICULATE NUCLEUS

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SUMMARY

1. Cat retinal ganglion cells may be subdivided into sustained and transient response-types by the application of a battery of simple tests based on responses to standing contrast, fine grating patterns, size and speed of contrasting targets, and on the presence or absence of the periphery effect. The classification is equivalent to the '*X*'/'*Y*' (linear/non-linear) subdivision of Enroth-Cugell & Robson which is thus confirmed and extended.

2. The sustained/transient classification applied to both on-centre and off-centre cells.

3. Lateral geniculate neurones may be similarly classified by the same tests. Occasional concentrically organized cells had a mixture of sustained and transient properties.

4. A technique for simultaneous recording from a geniculate neurone and one or more retinal ganglion cells providing its excitatory input showed that the connexions were specific with respect to the sustained/transient classification as well as the on-centre/off-centre classification. Most geniculate neurones are excitatorily driven only by retinal ganglion cells of the same functional type. In a few cases the inputs were mixed but only with respect to the sustained/transient classification.

5. Sustained retinal ganglion cells had slower-conducting axons than the transient type. The same was true for lateral geniculate neurones but in this case the distributions showed considerable overlap.

6. The sustained/transient classification is the functional correlate for the well-known segregation of optic nerve fibres into two conduction groups.

7. The pathways carrying sustained and transient information remain essentially separate from retina through the lateral geniculate nucleus to the striate cortex.

INTRODUCTION

It has been well known from the work of Kuffler (1952, 1953) that the receptive fields of cats' retinal ganglion cells possess a centre-surround type of organization. What is less well known is that there is another significant way in which the receptive fields may be classified in terms of functional properties of ganglion cells. Although there have been incidental observations which might have hinted at an alternative classification from time to time, the clearest demonstration so far has been presented by Enroth-Cugell & Robson (1966). They showed that receptive fields of both on-centre and off-centre concentric varieties could possess very different spatial-summation properties. Those ganglion cells for which summation over the receptive field was approximately linear they called X-cells; those for which the summation was very non-linear they classified as Y-cells. Both on-centre and off-centre varieties of each type were found although off-centre X-cells were rather uncommon. Sufficient numbers of all types were encountered to demonstrate a genuine new subdivision of function of cat retinal ganglion cells.

The non-committal $X-Y$ terminology introduced by Enroth-Cugell & Robson does not convey the essential nature of the new classification. Elsewhere, we shall describe a range of properties which correlate with the linear or non-linear summating behaviour of retinal ganglion cells. For present purposes, however, attention will be confined to a subset of the properties by which a neurone may be rapidly put in one or other class. On the basis of the tests applied it would be more appropriate to speak of a sustained/transient rather than an X/Y classification since the nature of the responses to standing contrast is one of the principal distinguishing features. This terminology also comes closer to describing the functional role of the respective families of ganglion cells.

At the next level in the visual pathway lateral geniculate neurones have been shown to possess receptive fields having a centre-surround organization with on-centre and off-centre varieties rather like their retinal counterparts (Hubel & Wiesel, 1961). The purpose of this paper is to extend the comparison between geniculate and retinal receptive fields along the dimensions of the $X-Y$ classification of Enroth-Cugell & Robson. In an initial series of experiments it emerged that the majority of the accessible geniculate neurones could be placed in one or other class as was the case with the retina. Thus it appeared that a segregation of function established in the retina was preserved to a considerable extent in the geniculate. In a further series of experiments, the detailed connexions underlying the segregation were investigated by simultaneous recordings of single geniculate neurones and those retinal ganglion cells providing excitatory drive

to them. These were more difficult experiments but they yielded direct information on the specificity of afferent connexions in the lateral geniculate nucleus.

METHODS

Experiments were carried out on adult cats (2–4 kg) in which anaesthesia was maintained with a mixture of 70 % nitrous oxide, 28·5 % oxygen, 1·5 % carbon dioxide given by artificial ventilation at 33 strokes/min, 10 ml./kg stroke volume. Immobilization was secured by infusion of gallamine triethiodide (Flaxedil) at 5 mg/kg. hr and D-tubocurarine 0·3–0·5 mg/kg.hr in 5 % glucose solution. Different animals varied in their sensitivity to the latter drug: in some, the lower dose rate failed to prevent slow, small eye-movements (detected by observing displacement of receptive fields), thus necessitating the higher dose; in others, the higher dose produced gradual dilation of the right pupil (non-operated eye in retinal and retinogeniculate preparations) with loss of direct and consensual reactions to light. This was thought to indicate relative over-dosage possibly by blockade of the ciliary ganglion (Guyton & Reeder, 1950). Although the state was compatible with long survival, we generally reduced the dose in these cases, and observed slow restoration of pupil mobility. The tubocurarine component was omitted from the infusion during the inactive stages of the experiment. In previously published work carried out with the same type of preparation (Barlow & Levick, 1969*a*, *b*; Levick & Zacks, 1970) relaxant was withheld periodically to check the level of anaesthesia. It was always found that the animals had brisk reflexes but no organized responses to pain-producing stimuli.

Preparation. Anaesthesia was induced with ethyl chloride; for surgical procedures it was continued with ether and then thiamylal sodium (Surital) after cut-down on the cephalic vein. The total dose given was usually from 20 to 60 mg depending on the cat's response. The trachea was cannulated and the vagosympathetic trunk severed on the left side (sometimes on the right as well). Sympathetic section aids ocular stability (Rodieck, Pettigrew, Bishop & Nikara, 1967). The carotid sheath and adjacent connective tissue were also cut. The corneas were protected with plastic contact lenses and an artificial pupil of area 7 mm^2 was routinely placed immediately in front of the contact lens after dilating the natural pupil and paralysing accommodation with atropine eye drops (1 %). Neosynephrine (2·5 %, Winthrop) was also employed when necessary to produce retraction of lids and nictitating membrane.

Retinal recording. The left eyeball was anchored to the foot-plate of a hydraulic micromanipulator by sewing a circular cuff of conjunctiva to a metal ring encircling the globe just behind the limbus. Tungsten-in-glass electrodes were introduced into the eye via a small cannula which penetrated the coats of the globe just in front of the equator. Single unit recordings were obtained from both the layer of optic nerve fibres and the layer of ganglion cells by advance of the electrode towards the retina from its vitreal side. In many experiments the outline of the optic disk and the approximate position of the area centralis were plotted for both eyes on a frontal tangent screen by direct projection of the retinal images through the sight-hole of a firmly fixed hand ophthalmoscope (Keeler). The location of receptive fields relative to the landmarks could then be readily determined by testing with hand-held wands on the same screen.

Geniculate recording. Standard Horsley–Clarke procedures were used to place tungsten-in-glass electrodes in the right lateral geniculate nucleus, optic radiation or optic tract. The electrode was inserted at the appropriate co-ordinates (Jasper & Ajmone-Marsan, 1960; Sanderson, 1971) after making a small craniotomy, reflecting dura and arachnoid, and sealing with agar (3 % in 0·9 % NaCl) to control pulsations.

Identification of recordings as originating from geniculate cells, radiation axons or tract axons was based on criteria given by Bishop, Burke & Davis (1962*a*) and Hubel (1960). Histological verification was established in some experiments by making electrolytic lesions and reconstructing electrode tracks from serial sections. When receptive fields of geniculate neurones were being tested, the eye not delivering excitatory drive was kept covered to avoid contamination from inhibitory effects (Sanderson, Darian-Smith & Bishop, 1969). The technique for obtaining simultaneous recordings from a geniculate neurone and a retinal ganglion cell providing its excitatory input has been described elsewhere (Cleland, Dubin & Levick, 1971).

Cortical stimulation. A linear array of four tungsten wires, each ensheathed in glass to within 2 mm of its electrolytically sharpened tip, was located in the striate cortex so that the individual electrodes were at Horsley–Clarke co-ordinates frontal: -3, -1, $+1$, $+3$; right lateral: all at 0·5–1·5. Each was pushed 2 mm into the cortex. In spite of their relative coarseness, each electrode could be used for recording a low amplitude 'swish' when contrasting targets were oscillated in the corresponding parts of the visual field: generally between 0 and 10° lateral and 5 to 15° below the projection of the area centralis for the coordinates given above. Detailed localization was helpful in planning the placement of the geniculate electrode.

For antidromic activation of geniculate cells rectangular pulses were applied to adjacent pairs of cortical electrodes either by coupling the output of a Tektronix 161 pulse generator via an isolation transformer or by direct connexion to the isolated output of a Grass S 5 stimulator. Both methods gave similar results. The pair of electrodes and polarity of stimulus yielding the lowest threshold were always used for obtaining measurements of geniculo-cortical conduction time. As expected, the visual field projection of the stimulating cathode of the pair with lowest threshold was usually the nearest to the location of the geniculate receptive field.

General. Amplification, display and recording arrangements by cathode-ray oscilloscope, loudspeaker and camera were conventional. Well isolated action potentials tripped a Schmitt trigger to produce pulses of standard amplitude and duration. The oscilloscope display of the spike was blanked by this 30 μsec pulse permitting immediate and continuous verification of correct triggering level. The pulse was also applied to a three-section low-pass, RC filter having an effective over-all time constant of 0·75 sec. The output of the filter was fed to a chart recorder (Heath EUW-20A) to provide a continuous record of the mean firing rate.

To provide a signal trace for records such as in Fig. 2 or Fig. 3, an optical system similar to a terrestrial telescope was mounted on a tripod with a pan-and-tilt head. Apertures could be placed in the intermediate image-plane and aligned on the experimental scene by direct viewing. The light passing the aperture could be deflected on to a 931A photomultiplier (RCA) by a hinged mirror.

For detailed testing of receptive fields it was convenient to work on a horizontal surface. A mobile mirror on a long arm was arranged in front of the animal so as to intercept the receptive field and adjacent visual field over a 30° region. The angle and distance of the mirror was arranged so that the receptive field was projected down on to a grey sheet on top of a table, the distance to the anterior nodal point of the eye being about 57 cm (thus 1 cm subtended about 1°). Diffuse room light provided a background luminance of about 10 cd/m^2 on the grey sheet. The non-intercepted part of the visual field was occupied by the large frontal tangent screen having a somewhat lower luminance.

Luminances were measured with a visual photometer (SEI, Ilford Ltd), the calibration of which was checked from time to time against a luminance substandard (Model 220-1A, Gamma Scientific Inc.) and an intensity substandard kindly provided by the National Standards Laboratory, C.S.I.R.O., Sydney. The average

reflectances over the visible range of white and black targets and the grey background screen were 0·9, 0·1 and 0·2 respectively.

A supplementary spectacle lens was usually necessary. The appropriate power was determined in the following manner. A range of powers was tried while gratings of various spatial frequencies were moved over the receptive field of a unit. The highest spatial frequency causing a detectable change in the maintained discharge ('acuity') was noted for each lens power. As expected, the acuity became greater as best focus was approach from both directions (see Fig. 1 in Barlow & Levick, 1965). Usually there was a range of lens powers for which the acuity was maximal. Although units with smaller centres reached greater acuities over narrower ranges of lens powers, the mid-points of the various ranges practically coincided. The lens power at the mid-point was the value used for the rest of the experiment.

RESULTS

Tests for sustained and transient retinal ganglion cells

In this section we describe four simple tests which were developed for separating retinal ganglion cells into sustained and transient response-types. This classification is equivalent to the division into *X*-cells and *Y*-cells made by Enroth-Cugell & Robson (1966) by virtue of differences in spatial summation properties.

Response to standing contrast. This test was usually carried out by unmasking, for about 1 min, a small target of appropriate contrast centred on the receptive field. Sometimes, it was done by projection as in Fig. 1 which compares the responses of typical sustained (*X*) and transient (*Y*) retinal ganglion cells. Both types showed a sharp increase in firing at moment of exposure but the discharge of the transient cell returned to, or near, the unstimulated maintained level within a few seconds. Some decay of the sustained cell's firing also occurred but the discharge always remained substantially above the maintained level as long as the target was present. When the target was covered the discharge of the sustained cell was strongly depressed below the original maintained level and slowly recovered over about 30 sec. The corresponding terminal event in the transient cell was weak and brief and had little effect on the mean discharge rate as recorded.

Certain precautions had to be observed to obtain the characteristic responses in this experiment. Control of retinal image quality was found to be important especially for the smallest-centred sustained type of ganglion cell. An eye with widely dilated pupil and uncorrected focus frequently yielded vague, weak responses which were poorly sustained. We routinely employed an artificial pupil (3 mm diameter) and the optimum spectacle lens correction determined from a unit's responses to grating patterns of different periods as described in Methods.

The size of the target was also important (see below) as was its con-

trast. In the case of on-centre cells we occasionally used a projected spot of light rather than the unmasking of a white target. If the spot were made too intense (e.g. 100 times threshold or more) the sustained component of a response was often greatly diminished. The occurrence of small eye movements was sometimes a serious disturbing factor particularly with small-centred cells. Such movements were inferred from a check of the position of the receptive field's centre with a small hand-held target moved over the screen. Displacements of the order of $\frac{1}{4}°$ or even up to $\frac{1}{2}°$ were found even though the eye was firmly stitched to an encircling ring at the limbus for the retinal preparation. Stability could often be improved by increasing the neuromuscular blockade (see Methods).

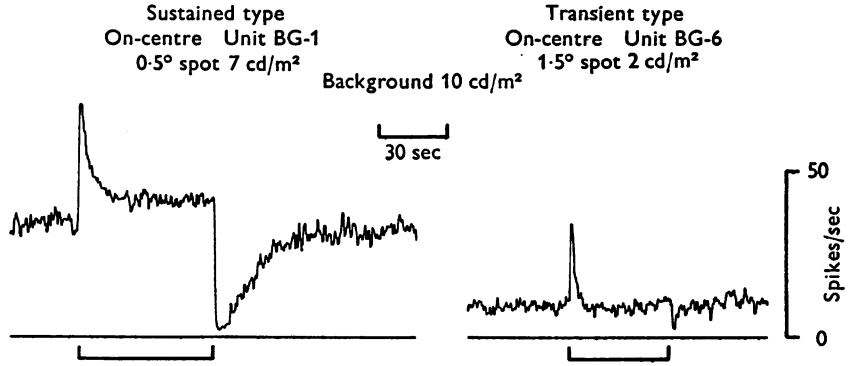

Fig. 1. Sustained and transient responses to standing contrast at the retinal ganglion cell level. In each case a centred test spot adding a luminance about 10 × threshold was turned on for the duration given by the thick bar beneath each record (time scale in centre). The irregular line is the graph of mean firing rate (calibration scale on right side) drawn by the chart recorder (see Methods). In each instance the spot used fell within the limits of the central zone of the receptive field. In the case of the transient cell (right), a spot 0·5° diameter at the same luminance (not illustrated) yielded a much weaker response still of the same transient form.

The above disturbing effects were to some extent the result of spread of the stimulus image on to the surround area of the receptive field either by optical blurring, scatter or actual displacement. A sequence of small eye movements could generate a train of transients having the appearance of an irregular sustained component in a truly transient cell; a single movement could greatly reduce the sustained component to a transient in a truly sustained cell. Physiological effects such as desensitization of the centre mechanism by intense light might also account for difficulties in obtaining a sustained component.

Response to grating patterns. This test is an adaptation of that described by Enroth-Cugell & Robson (1966). When a pattern of equally spaced

black and white parallel stripes (each 1° wide, period of pattern = 2°, spatial frequency = ½ cycle/degree) was moved across the receptive field, every ganglion cell responded with a shower of impulses as each bar of appropriate contrast passed the centre. It is only when the experiment was repeated with a sequence of patterns of increasing spatial frequency that a characteristic difference emerged between sustained and transient cells (Fig. 2). The response of the sustained cell continued to be a modulation of the maintained discharge about its mean level until the grating pattern became so fine as not to have any effect at all (about 4–6 cycles/deg). With the transient cell, however, the modulated character of the response was soon replaced by an unmodulated increase in the mean discharge rate which persisted while the movement continued (Fig. 2*C* right), but returned to the unstimulated level when the movement stopped. With finer patterns still, the response was reduced to a brief transient which occurred only at the moment that the pattern was jerked into motion (Fig. 2*F* right). Although the transient response to jerking often seemed feeble, it persisted to quite fine patterns, e.g. to 4 cycles/deg.

The above test is insensitive to the occurrence of residual eye movements but it does depend critically on retinal image quality. The detectability of the responses is determined by the extent to which the modulation of the grating image can displace the ganglion cell output outside the range of variation attributable to the unstimulated maintained discharge (Barlow & Levick, 1969*a*). If the image is so blurred that the modulation for all but the coarsest patterns is too low, the accessible behaviour is not very different for the two classes of cells. Another point, also mentioned by Enroth-Cugell & Robson, is to keep the temporal frequency of events at each point constant (about 2–3 c/s) to avoid contamination with time-dependent behaviour. This means that finer gratings must be moved more slowly; i.e. one should keep constant the number of bars per second passing each point. It was possible to miss the modulated response of a small-centred sustained cell by neglecting this caution.

Confirming Enroth-Cugell & Robson, we observed genuine quantitative differences in the extent to which individual cells could respond to progressively finer gratings. In the case of sustained cells, the variations were probably attributable to variation in size of the receptive-field centres (Wiesel, 1960).

Selectivity for size of targets and speed of motion. When a series of white or black targets was moved across the centre of the receptive field, it was observed that the response first increased with size of target up to a certain point and then decreased for larger targets. The existence of an optimum size for targets having the same contrast is precisely what one would expect on the basis of the area-threshold measurements which have been

published (Barlow, FitzHugh & Kuffler, 1957; Wiesel, 1960). The optimum size is a rough measure of the size of the receptive field's central zone. For the most of the sustained cells, the optimum target was $\frac{1}{2}$ or 1° in diameter,

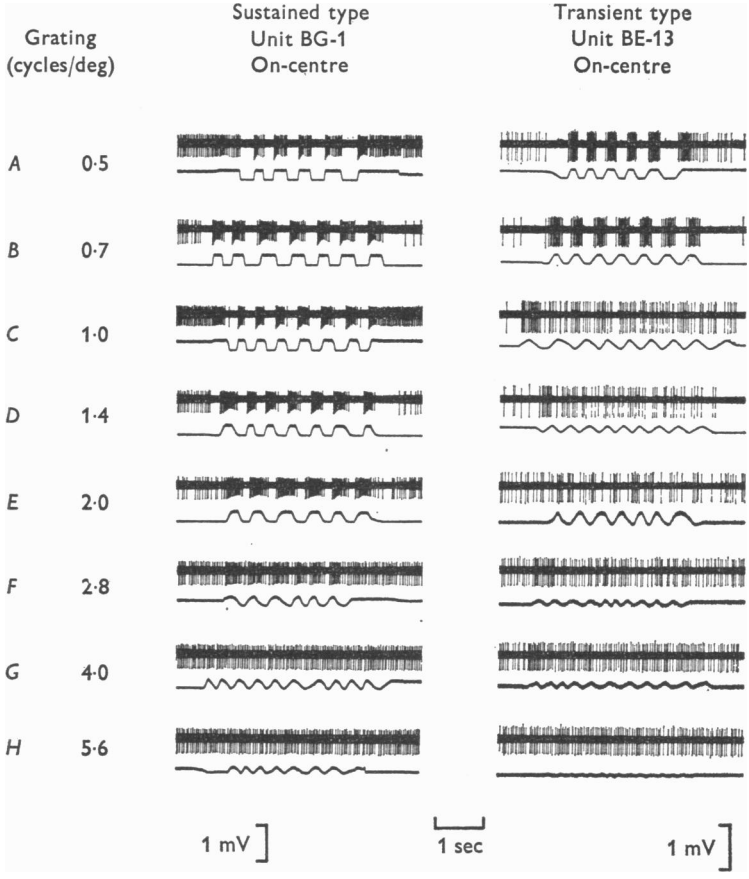

Fig. 2. Comparison of responses to moving grating patterns at the retinal level. In each record, the upper trace is the spike discharge (negativity up) of the cell (left column: sustained type; right: transient). The lower trace is the output of a photomultiplier receiving light via an optical system from the region of the receptive field; the system contained an oriented narrow slit centred on an intermediate image of the receptive field so as to make the output respond to passage of each bar (upward deflexion = increasing luminance) of the gratings. Spatial frequency of the patterns increases from top to bottom (numbers on left); finer patterns were moved more slowly so as to keep approximately constant the number of bars passing the receptive field per second (about 2 c/s). Orientation of the masking slit was critical for obtaining deep modulation of photomultiplier output to the finest patterns; it was non-optimal in the experiment on the right-hand side. The sustained cell had a simple modulated response down to the finest grating having any detectable effect.

whereas for transient cells, it was 1° or greater. No transient cells responded optimally to a $\frac{1}{2}$° target. More detailed information on receptive field sizes will be published elsewhere.

Differences between sustained and transient cells also extended along the dimension of target speed provided the contrast of the target was appropriate to the *surround* component of the receptive field. A typical comparison for on-centre cells is shown in Fig. 3. Whereas both types gave

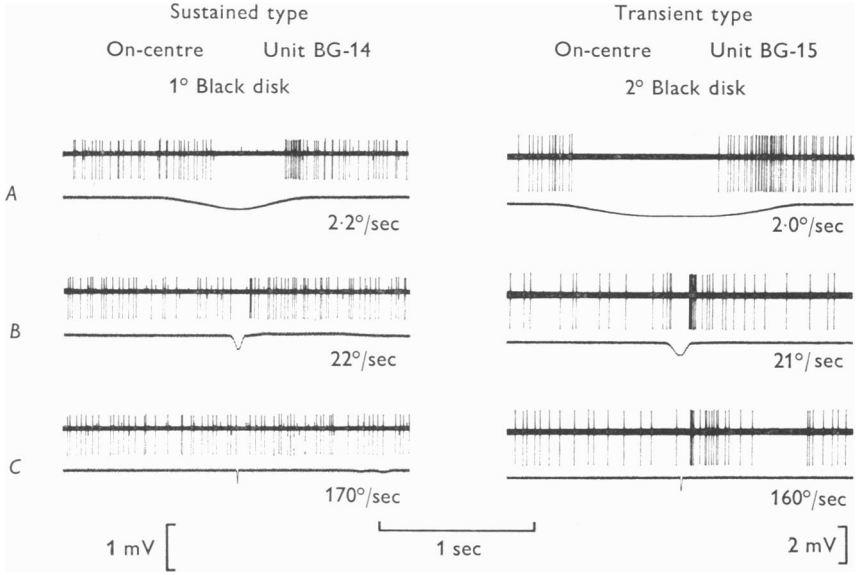

Fig. 3. Responses of sustained and transient on-centre retinal ganglion cells to black disks moved through the centres of their receptive fields at various speeds. Conventions as in Fig. 2. In this experiment a circular aperture was used in the image plane of the photomultiplier system to restrict its view to a zone centred on the receptive field subtending 1° at the eye. Speeds of the black disks were calculated from the photomultiplier deflexions and are shown at the lower right of each record. Although both cell types showed a pause in the maintained discharge for each transit, only the transient cell continued to emit a dense (though brief) burst of spikes at the highest speed.

a burst of spikes when a black disk moved out from the centre of the receptive field at slow (about 2°/sec) or medium (about 20°/sec) speeds, only the transient cells continued to respond strongly to fast (about 200°/sec) motion. Similar differential behaviour could be elicited with off-centre cells by the use of white disks. The distinctions were clearest with targets about twice or more times the optimum size for the centre. The short, densely packed burst of impulses from a transient cell gave a characteristic squeaking sound on the loudspeaker, a feature lacking in the sus-

tained type. If the contrast of the target used was appropriate to the centre component of the receptive field the distinction between the two types was less clear because sustained cells often gave detectable responses to fast motion.

Periphery effect. It has been shown (McIlwain, 1964; Levick, Oyster & Davis, 1965) that retinal ganglion cells can be weakly excited by visual stimuli applied well away from the conventionally defined receptive field consisting of centre and surround zones. This response, called the periphery effect, is elicited by continued movement of any large pattern and it consists of a gradual augmentation of the maintained discharge without any sharp timing relation to the oscillations of the stimulus. The effect was conveniently sought in the present experiments by having an observer simply walk behind the mirror which intercepted the receptive field (see Methods). The stimulus was thus the moving image of the observer falling on retina 15° or more from the centre of the receptive field.

TABLE 1. Classification of cell types

	Sustained		Transient		Mixed			
	On-centre	Off-centre	On-centre	Off-centre	On-centre	Off-centre	Other	Total
Retina	113 (33%)	92 (26%)	58 (17%)	80 (23%)	1 (0·25%)	2 (0·5%)	1 (0·25%)	347
LGN	56 (30%)	39 (21%)	36 (19%)	23 (12%)	10 (5%)	10 (5%)	15 (8%)	189

The periphery effect was obvious and strong with nearly all transient cells, but weak or absent with sustained cells. In some cases the test was made in the presence of a subthreshold stimulus applied to the receptive field proper (stationary fine grating, flickering spot of light); a feeble periphery effect could thus be intensified and more easily revealed.

Summary. The application of the foregoing tests enabled us to classify a sample of retinal ganglion cells drawn from a region within 30° of the area centralis but excluding the area centralis itself. The results are given in Table 1. Most of the units fitted into either the sustained or transient class. Only three had a mixture of features. A further unit genuinely lacked the classic on-centre or off-centre concentric organization (Kuffler, 1952, 1953). This unit had an on-off receptive field and behaved in some respects like the local-edge-detector ganglion cells in the visual streak of the rabbit's retina (Levick, 1967).

Sustained and transient lateral geniculate neurones

For the next series of experiments we asked whether or not lateral geniculate neurones could also be classified as sustained or transient in the same way as the retinal ganglion cells. The question is not trivial: it is known, for example, that some integrative action does take place in the lateral geniculate nucleus (Hubel & Wiesel, 1961); also, part of the retinal output is destined for the superior colliculus (Hayashi, Sumitomo & Iwama, 1967), raising the possibility of a segregation of function with respect to destination.

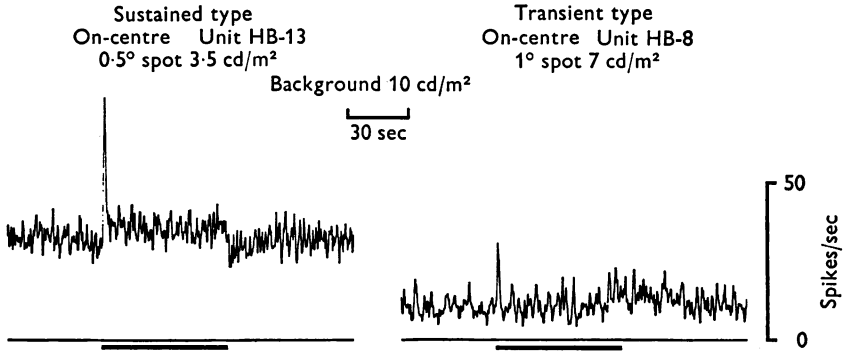

Fig. 4. Sustained and transient responses to standing contrast at the geniculate level. Same conventions as in Fig. 1. In each case the centred spots of added light were about 10 × threshold for the respective cells, and fell within the limits of the central zones. On the left there was a definite though small sustained response for the duration of the stimulus (black line below). With the transient cell on the right, there was no combination of area or luminance of the spot, including that illustrated, which could produce a sustained response.

We employed the same four tests described earlier. The result was that lateral geniculate neurones could, with a few exceptions, be separated into sustained and transient response-types. Figs. 4, 5 and 6 are companions at the geniculate level to Figs. 1, 2 and 3 for the retina, illustrating behaviour of typical members of the sustained and transient classes. It should be emphasized that the sustained component of a response to standing contrast (Fig. 4) never appeared as prominently at the geniculate level as it did at the retinal. This may be related to the observation that the geniculate maintained discharge in the absence of a stimulus was also generally less than the retinal under the prevailing conditions of illumination. Residual quantitative differences between Figs. 5, 6 on the one hand and Figs. 2, 3 on the other are partly attributable to variation in centre sizes mentioned earlier. In addition, it was observed that the

range of gratings yielding the unmodulated increase of firing in transient units was usually more restricted at the geniculate level, so that the behaviour became: modulated response to coarse patterns, brief discharge to onset of motion for finer patterns (Fig. 5, right column).

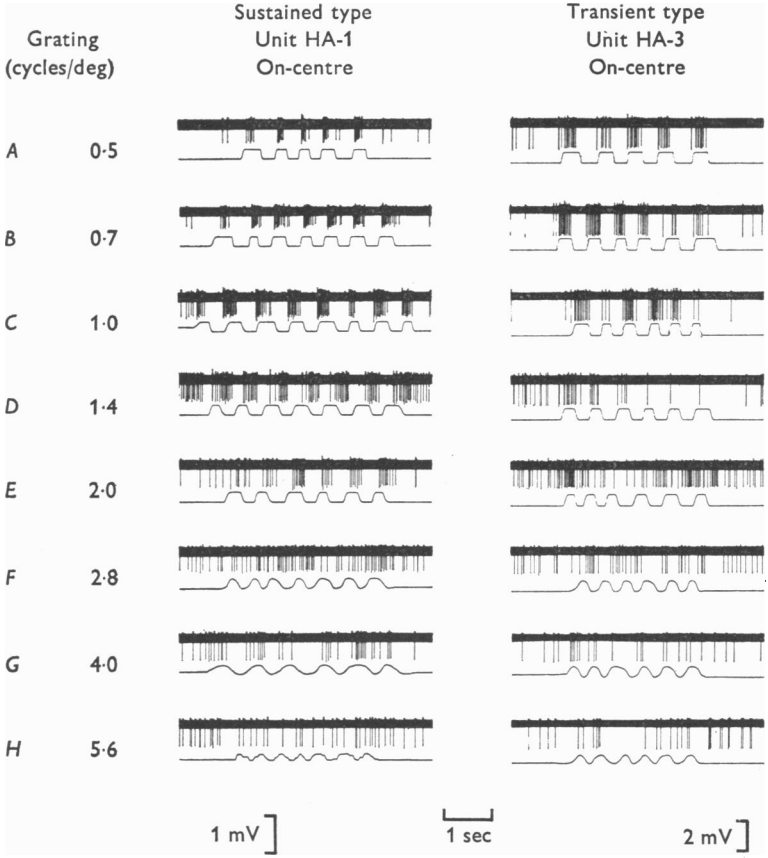

Fig. 5. Comparison of responses to moving grating patterns at the geniculate level. Conventions as in Fig. 2. The particular sustained cell used here did not resolve as fine a grating as the sustained retinal ganglion cell of Fig. 2. However, other examples did resolve as effectively.

In general, it was more difficult to obtain clear-cut results at the geniculate level. Although the maintained discharge of geniculate neurones covered a lower range of values than that of retinal ganglion cells, it was more irregular (compare Fig. 4 with Fig. 1). Therefore, responses would have to be relatively stronger to rise out of the range of variation of the unstimulated discharge. Another problem was that the responsiveness of geniculate neurones sometimes varied considerably during the experiment.

This effect appeared to be related to changes in the character of the maintained discharge: whenever it became dominated by infrequent, brief, clusters of impulses, the responses to optimized stimuli waned and any sustained components became transient. This type of maintained discharge has been associated with 'sleep' (Hubel, 1960) or more particularly, with 'slow-wave sleep' (Sakakura & Iwama, 1967). Factors other than the general state of the brain must also play a part since we could induce the

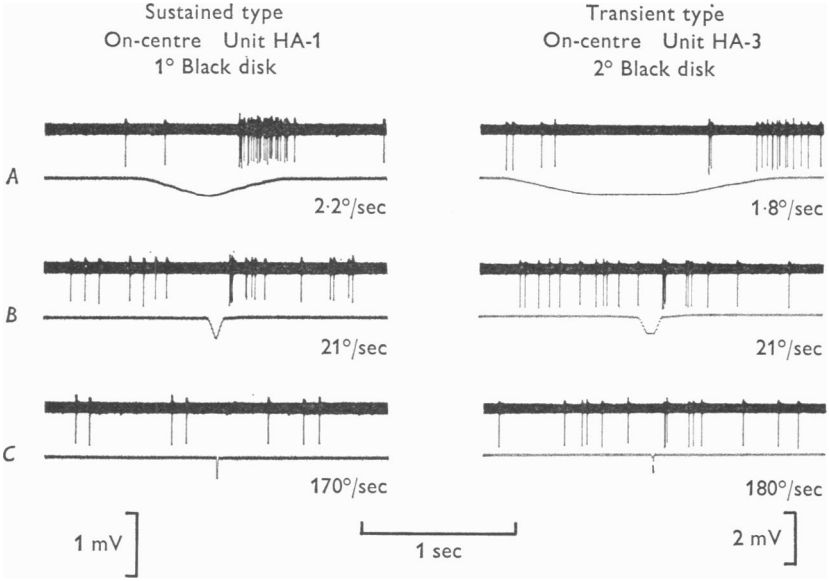

Fig. 6. Responses of sustained and transient on-centre lateral geniculate neurones to black disks moved through the centres of their receptive fields at various speeds. Same arrangements as for corresponding retinal experiment of Fig. 3. Note presence of a burst of spikes from the transient cell at the fastest speed.

clustered firing pattern by applying local stimuli which would be expected to cause strong depression of the discharge in the excitatory retinal inputs to the geniculate neurone. By postponing data-collection during the spontaneously occurring periods of strongly clustered firing, unequivocal results to the tests could usually be obtained.

Extra surround region. Even though all the precautions outlined earlier for the retinal testing were taken there was an additional effect tending to obscure the results at the geniculate level. A proportion of the neurones responded weakly or not at all to grating patterns of all frequencies. If, however, the view of the grating was restricted to a zone 2–4° in diameter centred on the receptive field, the familiar pattern of responses returned. The restricted field was achieved by placing a stationary sheet of grey

card containing a 2–4° hole immediately in front of the grating. The size of hole used was selected by trial and would have been large enough in each case to have included the centre and a substantial proportion of the antagonistic surround of the receptive field. Such masking had little effect at the retinal level. It therefore appeared that some geniculate receptive fields had an extra surround region which could be brought into action by coarse or fine grating patterns and which had an inhibitory action on the responses to simultaneous stimulation of the centre. Comparable observations have been made by Hubel & Wiesel (1961). Further analysis of this behaviour will be presented elsewhere.

Periphery effect. Although most geniculate neurones of the transient type had an easily demonstrated response to this test, there were some in which no excitatory effect could be found, even when a subthreshold stimulus was applied to the receptive field centre as described earlier. It is possible that the periphery effect may be inhibitory in some cells as suggested by McIlwain (1964), perhaps because of inhibitory mechanisms in the lateral geniculate nucleus. It would have required lengthier analysis to detect such effects against the relatively slow and highly irregular maintained discharge of geniculate neurones.

Summary. The results of classifying geniculate neurones are collected in Table 1. As with the retinal ganglion cells most units were either transient or sustained, a few had mixed properties (see later) and fewer still lacked the familiar concentric on-centre or off-centre type of receptive field. Some of these may have been 'I-cells' (Burke & Sefton, 1966). Transient and sustained cells were found in all three layers of the lateral geniculate nucleus. There was insufficient data to say whether the proportions were significantly different among the layers.

Simultaneous recordings at retina and geniculate

The implication of the finding that geniculate neurones could be classified in the same way as retinal ganglion cells is that there should be a segregation of optic tract endings on geniculate neurones according to function. In the next series of experiments, we investigated this directly by recording simultaneously from individual geniculate neurones and from the ganglion cells which provided their excitatory input. Concurrent recordings also have the advantage of providing a control against variation in the state of the preparation during an experiment and possible differences from animal to animal.

Identification of excitatory inputs. After establishing single unit recording in the lateral geniculate nucleus we systematically explored the corresponding region of the contralateral retina. Under favourable conditions it was possible to isolate sequentially one or more ganglion cells having the

following property in common: a certain proportion of impulses from the geniculate neurone was preceded at a short and almost constant time interval by a proportion of the impulses from the ganglion cell. Fig. 7 illustrates a typical situation. Both beams of the oscilloscope were triggered by impulses from the retinal ganglion cell (RGC lower trace) and several sweeps were superimposed. The upper trace shows that ganglion cell spikes were followed by geniculate impulses occurring 2·7–3·2 msec later, but not on every occasion. In the case of some geniculate neurones, nearly every impulse of the discharge could be accounted for by a preceding impulse in the ganglion cell recording. Where accountability fell

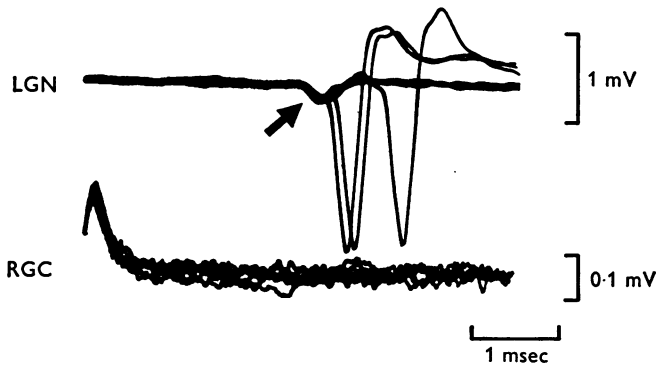

Fig. 7. Simultaneous recording of an LGN neurone and one of its retinal ganglion cell (RGC) drives. Both oscilloscope beams were triggered by the occurrence of an RGC spike, a number of which are shown superimposed in the lower trace. The upper trace shows the output of the LGN neurone; every RGC spike initiated an 'S-potential' (arrow) at the LGN neurone. Three of these 'S-potentials' are seen to lead to the generation of spikes. Unit-pair RPG-2_1.

well short of 100%, further retinal search usually yielded one or more additional ganglion cells whose impulses had a similar sharp timing relationship to the geniculate impulses.

For present purposes retinal ganglion cells having the above property will be considered to be the functionally significant excitatory inputs ('drives') to a particular geniculate neurone. Further details have been given elsewhere (Cleland, Dubin & Levick, 1971). In the remainder of this section we compare the functional properties of geniculate neurones with those of their retinal drives.

Functional segregation. The general picture that emerged from a study of ninety-seven geniculate neurones was that a particular cell received excitatory input from one or more ganglion cells only of the same functional type. This was true for both the on/off as well as the sustained/transient

classifications. The result was most clearly demonstrated with those geniculate neurones (eight units, 8% of the sample, six sustained and two transient types) which had just a single drive. Multiple-input neurones also generally conformed to the pattern but here certain qualifications must be stated. There were many instances where the retinal search was terminated prematurely by loss of the geniculate recording. In most of these cases the drives found were of the same functional type as the geniculate neurone and had very similar conduction times. Of the ten geniculate neurones where the search seemed complete, eight had drives all of the same functional type (four sustained and four transient types).

There were a few exceptions to the above general picture, all related to the sustained/transient classification, and all involving multiple-input cells. Two types have been observed; either: geniculate testing suggested the sustained class, but one of the retinal drives had transient properties; or the converse. What is the input relationship for geniculate neurones having mixed properties (Table 1)? Two classes have been observed. In the most common case, both a sustained and a transient type of retinal drive were found. In one instance, the one retinal drive found had mixed properties itself.

Conduction times

Retino-geniculate latency. An interesting product of the experiments with simultaneous recording was the measurement of the time taken for an impulse initiated at the retinal ganglion cell to reach a geniculate neurone. A commonly occurring feature of the geniculate cell recordings was the presence of the 'S-potential' (arrowed in Fig. 7; Bishop, Burke & Davis, 1962*a*, *c*; 'optic-tract synaptic potentials' of Hubel & Wiesel, 1961) which is believed to be the extracellularly recorded excitatory post-synaptic potential of the geniculate neurone. Its timing relative to the onset of the impulse in the retinal ganglion cell was always stable to within 0·1 msec whereas the geniculate cell's impulses showed substantial jitter, usually of the order of 0·5–1 msec. Impulses were observed to arise even on the falling phase of the S-potential. This is understandable if one assumes that the close extracellular electrode recorded a voltage proportional to the subjacent membrane current (Freygang, 1958; Freygang & Frank, 1959). The recording would thus have contained a substantial component of the time-derivative of the trans-membrane excitatory post-synaptic potential (cf. Fig. 19*C*, *D*, *E* in Eccles, 1957).

Conduction time was measured from the beginning of the ganglion cell deflexion to the beginning of the S-potential by direct reading of an oscilloscope display like that yielding Fig. 7. The measurement thus included synaptic latency (Grundfest, 1959). On some occasions the geniculate impulse was recorded as an initially negative-going spike and the

S-potential was not observed. The procedure then was to measure to the beginning of the earliest-occurring related negative spike. On the assumption that the negative-going spike represented the same event as the initially positive-going impulses of Fig. 7, the latter measurements would include an extra time for impulse-generation of about 0·3 msec.

The frequency histogram of retino-geniculate latencies is given in Fig. 8. It is immediately obvious first, that ganglion cells fall into two distinct groups, and secondly, that the units classed as transient occupy the fast-conducting group while those classed as sustained occupy the slow.

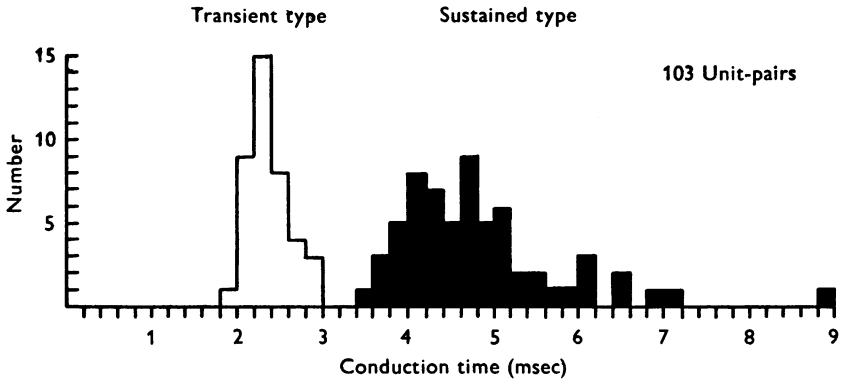

Fig. 8. Frequency histogram of retino-geniculate conduction times. Note that all transient retinal ganglion cells (white bars) fell into a group with short conduction times; all sustained cells (black bars) made up a group with longer conduction times.

Geniculo-cortical latency. Since the sustained/transient classification correlated so well with axonal conduction time for the retinal ganglion cell, the question naturally arose whether a similar correlation also existed at the next level. In the final series of experiments we therefore coupled a functional assessment of geniculate neurones with antidromic activation from the visual cortex.

We adapted the criteria of Bishop, Burke & Davis (1962*b*) for determining that activation of a geniculate neurone was antidromic rather than transsynaptic. The tests were: (*a*) demonstration of a period following an orthodromically occurring impulse during which the geniculate cell was inaccessible to cortical stimulation, initially because of collision of impulses on the axon and later because of refractoriness of the axon endings in the cortex; (*b*) altered shape of geniculate cell's impulse (no S-potential; prominent step on positive phase of initially positive wave form); (*c*) latency shorter than about 5 msec; (*d*) minimal timing jitter ($< 0{\cdot}1$ msec) with suprathreshold cortical stimulation; (*e*) sharp threshold (Fig. 9*A*) and minimal shortening of latency ($\sim 0{\cdot}15$ msec) as a function of stimulus strength (Fig. 9*B*); (*f*) response never contained more than a single impulse in the first 10 msec at any stimulus strength (apart from the chance occurrence of an orthodromic impulse from

the maintained discharge). Activation having sharply different properties was also observed and was believed to be transsynaptic: the inaccessible period was no longer than the minimum period for a pair of cortical shocks each to produce an impulse; increase of cortical stimulus increased the number of impulses elicited and considerably shortened the latency of the first; timing of the response was very variable; latency for a stimulus evoking just one impulse was usually longer than 5 msec.

To establish uniform conditions we roughly determined the weakest stimulus that would cause an occasional impulse in the geniculate cell. The intensity was increased 2·5 times and the latency measured from the beginning of the artifact to the beginning of the impulse. It was not sufficient to use the intensity yielding 50 % probability of response, because the plateau height of the probability-of-firing curve (Fig. 9*A*) was very variable, sometimes not even reaching 50 %. With intact retinas, the spread of the impulse into the geniculate neurone was evidently controlled by factors not directly related to cortical stimulus intensity, for example, by fluctuation of inhibitory input.

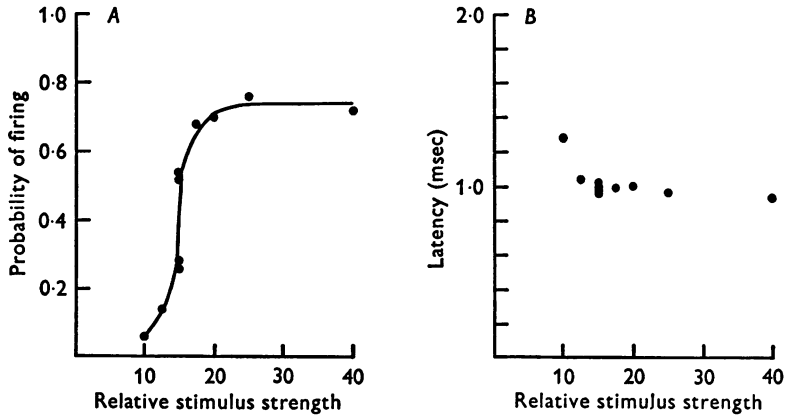

Fig. 9. Antidromic activation of a geniculate principal cell. *A*. Probability of impulse-invasion of cell as function of strength of 100 μsec stimulus applied to axonal endings in striate cortex. Each point is based on responses to fifty trials. Note the sharp threshold and steep rise to a plateau probability of invasion substantially less than 1·0. *B*. Antidromic geniculo-cortical latency as a function of stimulus strength. Same unit as in *A*. Each point represents the mean of latencies for the successful invasions which occurred at the particular strength. Apart from the high point at the weakest level, there is only minor shortening of the latency with increasing stimulus strength. Unit GY-9: off-centre, sustained type.

The frequency histogram of geniculo-cortical latencies is shown in Fig. 10*B*. It agrees well with that of Bishop *et al.* (1962*b*). When the graph is subdivided according to the sustained (black)/transient (white) classification as tested at the lateral geniculate level, there is a definite tendency for sustained cells to have the longer latencies. Statistical analysis confirmed that the mean latencies of the two classes (sustained: 1·61 msec ±

0·79 S.D.; transient: 0·75 msec ± 0·16 S.D.), were significantly different at the 0·005 level (*t* test).

Combined latency measurements. Our data includes thirty geniculate neurones where conduction times of the post-synaptic and presynaptic axons were measured together. The scatter diagram of one plotted against the other is shown in Fig. 10*A*. The filled symbol/open symbol (sustained/transient) convention here refers to characterization at the retinal level.

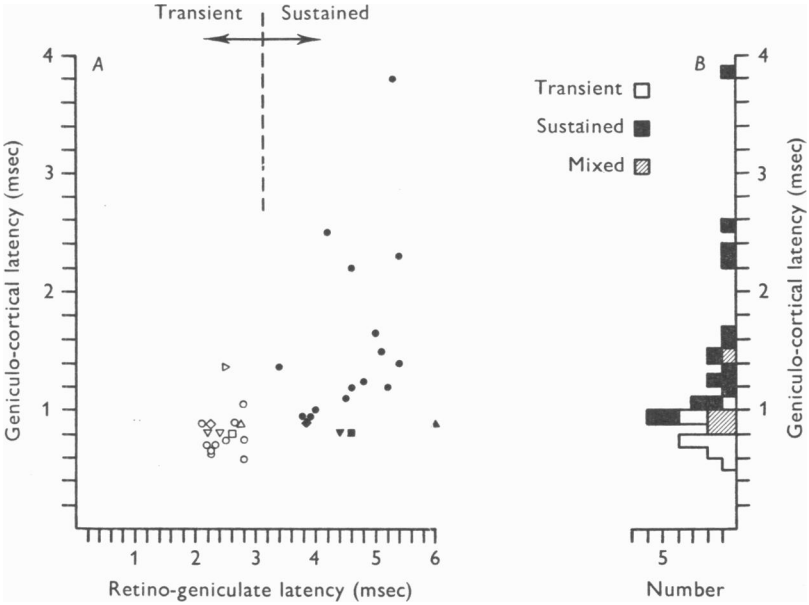

Fig. 10. *A*. Scatter diagram of the antidromically determined geniculo-cortical latencies of individual LGN neurones versus the retino-geniculate latencies of their simultaneously recorded ganglion cell inputs. Open symbols indicate retinal inputs of the transient-type; filled symbols indicate inputs of the sustained type. Non-circular symbols indicate drives to LGN neurones with mixed inputs, where similarly shaped symbols indicate inputs to the same neurone. *B*. Frequency histogram of geniculo-cortical latencies of the LGN neurones plotted in *A*. Open blocks indicate transient LGN neurones; filled blocks indicate sustained LGN neurones; hatched blocks indicate mixed LGN neurones.

It is obvious that faster-conducting optic axons generally make synapses on geniculate cells also having faster-conducting axons. A similar result has been obtained by electrical stimulation of the optic chiasm and visual cortex, in the cat by Stone and Hoffmann (personal communication) and in the rat by Noda & Iwama (1967).

The retinal drives to five geniculate cells having mixed input are shown

with special symbols in Fig. 10*A*. The conduction times of the geniculate axons were in the range corresponding to the type of the main retinal drive.

DISCUSSION

Whereas a cell at the retinal or geniculate level can generally be classified as on-centre or off-centre by a few seconds' work with hand-held wands, the same is not true for the sustained/transient classification. We found it necessary to apply several tests and even then units with intermediate properties were encountered. It may therefore be objected that we have artificially imposed a dichotomous classification on a single family of neurones with essentially continuously graded properties. For example, the sustained property might progressively become supplanted by the transient as one proceeds to ganglion cells with larger centres. The argument for a genuine dichotomy rests on the following points.

First, although units with intermediate properties did occur, the majority could be classed unambiguously as sustained or transient. Secondly, the class of a cell simply could not be predicted from the size of its receptive field's centre. There were examples of cells classed as transient with smaller centres than others classed as sustained. Thirdly, the association of ganglion cell class with retino-geniculate latency together with the clear-cut grouping of latencies indicates a structural substrate for dichotomous classification. This point does not apply directly to geniculate neurones because geniculo-cortical latencies were monomodally distributed. Nevertheless, the argument does extend to geniculate neurones because the majority received excitatory input only from ganglion cells of the same functional class. The number of exceptions (mixed inputs) is relatively greater at the geniculate level, but still not sufficient to blur the distinctness of the classification.

Optical artifacts, damage by the recording electrode and progressive changes in the state of the preparations have been suggested as factors determining the classification. These are readily ruled out. Sustained and transient cells were found at all stages of experiments, sometimes simultaneously recorded. Recordings made from axons rather than cell bodies (intraocularly, in the optic tract or optic radiation) gave similar results, thus excluding damage, pressure and scattered light.

It cannot yet be said whether the sustained/transient classification is applicable over the full range of adaptation levels. In the present experiments, only a single level was used; this would correspond approximately to the middle of the range over which the Purkinje shift occurs (Barlow & Levick, 1968). There is evidence to be presented elsewhere which suggests that the transient property is associated with the surround component of

the receptive field. Since the effectiveness of the surround varies with adaptation level (Barlow & Levick, 1969*b*), the distinctions made in this paper may diminish at low background illumination. The level used was well into the range where surround components are active.

Conduction times

A principal result of this paper was the discovery of a functional correlate of the fast and slow groups of fibres in the cat's retino-geniculate pathway: cells classed as transient by testing the receptive fields had axons in the fast-conducting group, those classed as sustained had slow axons. G. H. Bishop & O'Leary (1940, 1942) described two fibre groups going to the lateral geniculate nucleus but these were most clearly demonstrated by Bishop, Jeremy & Lance (1953) by stimulating the optic tract and recording the antidromically conducted compound action potential in the optic nerve suspended in air. The ratio of means of retino-geniculate latencies for the two groups (Fig. 8) was $2{\cdot}3/4{\cdot}8 = 1/2{\cdot}1$; this is sufficiently close to the corresponding value for electrical stimulation of the optic nerve with field recording in the contralateral geniculate (1/2·5, Bishop, 1953) to enable identification of our two groups with the t_1 and t_2 potentials of Bishop (summarized in Bishop, 1964). The magnitudes of our latencies were greater because of slowed conduction in the intraocular unmyelinated segments (Dodt, 1956).

G. H. Bishop & Clare (1955) thought that the slower of the two groups going to the LGN synapsed only in layer B and the relay cells did not project to the cortex but to the lateral nucleus of the thalamus. Our results are at variance on both points: both sustained and transient geniculate neurones were found in all layers and both types could be antidromically activated from area 17 of the visual cortex.

Functional significance

There have been previous attempts to determine the physiological significance of groups of cat optic axons conducting at different speeds. Chang (1952) thought that three groups of fibres would carry the components of trichromatic colour vision but this scheme in its elementary form was inconsistent with results of Motokawa, Oikawa & Tasaki (1957) who showed much more obscure relations between conduction velocity and colour-coding. Lennox (1958) also presented evidence that the responses of slow and fast units behaved differently to stimulus light of different colours. Later, Fukada, Motokawa, Norton & Tasaki (1966) found that the critical fusion frequency for flickering light was positively correlated with conduction velocity. In the rat, Sumitomo & Iwama (1967, 1968) were able to correlate ongoing discharge and responsiveness to the frequency of

flickering light in lateral geniculate cells with the conduction velocity of the presynaptic input. In none of these studies has detailed attention been given to receptive field structure apart from attempted classification in terms of the responses to diffuse light flash. In this respect our work is in agreement in showing no convincing relation between the on-centre/off-centre classification and retino-geniculate conduction time. In the monkey, Gouras (1969) has found that colour-coded retinal ganglion cells have well-sustained responses to steady stimuli ('tonic' behaviour) and slowly conducting axons, in strong contrast to non-colour-coded cells which have transient responses ('phasic' behaviour) and faster-conducting axons. It would be interesting to pursue the experimental comparison of cat and monkey further.

From the tests described here and the work of Enroth-Cugell & Robson (1966), it can be inferred that the sustained (*X*-type) retinal ganglion cells are capable of signalling steady, local differences of illumination. The transient (*Y*-type) cells could constitute an initial stage in the development of a specific sensitivity to motion because of their responsiveness to either large objects moving at some distance from their field centres (periphery effect) or any-sized objects suddenly crossing or moving within their receptive fields' centres or surrounds. For smaller objects moving slowly, both types have in common the properties of localization (response magnitude increases with proximity to centre of receptive field) and identification (net increase of impulse output for lighter objects in on-centre cells, and for darker objects in off-centre cells).

The specialized information is kept largely separate after passage through the lateral geniculate nucleus and conveyed at least to area 17 of the visual cortex as shown by antidromic activation of both types of geniculate neurones from that region. According to Hayashi *et al.* (1967) a substantial proportion of the faster-conducting optic tract axons branch to provide input to the superior colliculus as well as the lateral geniculate nucleus. Thus the transient system may provide a basis for the elaboration of the high-speed direction-selective property described for many collicular neurones (McIlwain & Buser, 1968).

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