J. Physiol. (1971), **213**, *pp.* 475–494
With 5 *text-figures*
Printed in Great Britain

CHROMATIC SENSITIVITY AND SPATIAL ORGANIZATION OF CAT VISUAL CORTICAL CELLS: CONE-ROD INTERACTION

BY P. HAMMOND

From the Medical Research Council Group, Department of Communication, University of Keele, Keele, Staffordshire

(*Received 17 September 1970*)

SUMMARY

1. Colour sensitivity and spatial organization were determined for the dominant-eye receptive fields of thirty-eight simple or complex cells in cat primary visual vortex. Receptive fields were all from the cortical area associated with central vision. Each cell was investigated with threshold or suprathreshold monochromatic stimuli, under scotopic, low and high mesopic adaptation.

2. The Purkinje shift, well defined for all units, was consistent with dual input from each of only two receptor mechanisms, viz. 556 nm cones and 500 nm rods. With change of adaptation level there was a systematic change in the peak sensitivity of spectral response curves to suprathreshold monochromatic stimuli, equated for quantum flux but of different wave-length. Equally with change of adaptation, the relative shift in threshold between wave-lengths selective for cone or rod activation was in close agreement with the change predicted from the Dartnall nomogram curves for visual pigments 556 and 507 respectively.

3. For ganglion cells with concentric fields rod input derives from a spatially larger area than cone input. Rod field centre and rod field surround are substantially larger than the corresponding centre and surround for cones (Andrews & Hammond, 1970*b*). For cortical cells a conclusive comparable change could only be demonstrated for one simple unit. Its receptive field consisted of a horizontal excitatory stripe with asymmetric inhibitory flanks. When light-adapted the weaker, upper flank was functionally undetectable, indicative of purely rod input to this side-band, and the preference for upward movement was enhanced.

4. No difference in receptive field configuration, or in spatial extent of input mediated by cones or by rods, was detected for any other unit. The discrepancy between retinal and cortical findings is discussed. It is inferred that cortical fields are compounded essentially by convergent input from geniculate cell field-centres.

INTRODUCTION

In cat the Purkinje shift from 556 nm (photopic) to around 500 nm (scotopic) is well established both behaviourally and from retinal neurophysiology (Granit, 1943, 1945, 1955; Gunter, 1952, 1954; Weale, 1953; Barlow, Fitzhugh & Kuffler, 1957*a*). The increment threshold measurements of Daw & Pearlman (1969) for single units in LGN, optic tract and optic radiations are indicative of a single class of cones in the retina (peak 556 nm), and a single class of rods (500 nm). Our own results, entirely from fibres within the optic tract, are in agreement with theirs (Andrews & Hammond, 1970*a*).

The receptive fields of cat retinal ganglion cells are concentrically organized and basically of two types, on-centre or off-centre with an antagonistic surround (Kuffler, 1953). We found that the great majority of optic tract fibres with concentric fields received mixed input from 556 nm cones and 500 nm rods to both field centre and surround; only 4 % received input purely from rods (Andrews & Hammond, 1970*a*, *b*). All units reported by Daw & Pearlman (1969) received mixed cone-rod input.

Behaviourally the cat is capable of making colour discriminations (Mello & Peterson, 1964; Sechzer & Brown, 1964; Meyer & Anderson, 1965). Earlier, in the absence of neurophysiological evidence for more than one type of cone receptor, we worked on the hypothesis that colour discriminations in cat must be based on mesopic interaction between 556 nm cones and the rods. Barlow, Fitzhugh & Kuffler (1957*b*) demonstrated a spatial change in retinal receptive field organization during dark-adaptation. The antagonistic surround of concentric (rod) fields became progressively weaker, and in total dark-adaptation was functionally lost. In the mesopic range we found an additional change in spatial organization related to the changeover from cone to rod vision (Andrews & Hammond, 1970*b*). For optic tract fibres the receptive field centre was larger for rods than for cones, as was the surround. The result, in particular, was an overlap between rod field-centre and cone field-surround giving, in a sense, an area of each receptive field with spectral opponency between cones and rods. We suggested that this opponency coupled with differences in latency and time course of cone and rod events (Gouras & Link, 1966; Gouras, 1967, 1968; Hammond, 1968; Andrews & Hammond, 1970*b*), might form the basis of the cat's ability to make colour discriminations in the mesopic range.

In a parallel series of behavioural studies Pearlman and Daw have shown that cats trained to discriminate colours under mesopic conditions retain this ability at adaptation levels adequate to saturate the rods (Pearlman & Daw, 1970; N. W. Daw, personal communication). These

results impute more than one cone mechanism. Further neurophysiological recordings from 118 LGN and optic tract units under photopic conditions revealed three cells in LGN exhibiting cone-cone opponency between 450 and 556 nm cones (Pearlman & Daw, 1970). Earlier work by these authors on 81 units from LGN, optic tract and optic radiations had failed to show up the 450 nm cone mechanism (Daw & Pearlman, 1969), as had our own studies on 122 optic tract fibres (Andrews & Hammond, 1970*a*, *b*). Thus overall the proportion of units with 450 nm cone imput, additional to that from 556 nm cones, is extremely small – rather less than 1 %. Contrary to expectation none of the cone–cone opponent cells were located in the region of central vision, though it is of significance that all three were isolated in layer B of LGN (Pearlman & Daw, 1970). It would seem likely, therefore, that photopic colour discrimination in cat is of relatively minor importance.

However, the fact that the cat does possess both an underlying neural organization of functionally opponent elements and the behavioural ability to make colour discriminations strengthens our earlier concern about the validity of assessing visual cortical unit activity with black-and-white stimulation and without careful control of the level of adaptation. It has already been shown that some cells in monkey lateral geniculate and cortex handle colour and white light in quite different ways (Wiesel & Hubel, 1966; Hubel & Wiesel, 1968). In the cat we predicted that the spatial and chromatic organization of cone-rod information at the retinal level (Andrews & Hammond, 1970*a*, *b*), and the chromatic organization of cone–cone and cone–rod information from retina and LGN (Daw & Pearlman, 1969; Pearlman & Daw, 1970), might well be reflected at the cortical level.

This paper describes the results from monochromatic stimulation of a sample of simple and complex cells from cat Visual 17 under careful control of levels of adaptation. Attention is focused on the Purkinje shift, spatial and functional changes in receptive field organization, and the possibility that input to a few cells might involve more than one class of cones.

METHODS

Preparation. Ten adult cats (range 2·1–4·0 kg) were prepared acutely, using one of three anaesthetic procedures. One animal was anaesthetized initially with intraperitoneal Nembutal (40 mg/kg); supplementary doses (7 mg/kg) were given as necessary. One animal was induced with halothane/oxygen and maintained on intravenous chloralose (50 mg/kg initially, supplemented at 10 mg/kg as necessary). Dosage rates in both cases were established before administration of muscle relaxant. The remaining eight animals were given atropine sulphate premedication (0·15 mg) and surgery was performed under halothane/oxygen. On completion of

surgery one of these animals was maintained on 80%/20% N_2O/O_2 supplemented with halothane as necessary; seven were maintained on 70%/30% or 50%/50% N_2O/O_2 supplemented with intravenous neuroleptanalesic agents, droperidol (0·2 mg/kg, Droleptan, Janssen Pharmaceuticals) and phenoperidine hydrochloride (0·1 mg/kg, Operidine, Janssen Pharmaceuticals), with maintenance doses of phenoperidine hydrochloride (0·02 mg/kg) after 1 hr and at intervals of 2–3 hr.

Temperature was maintained at 38–38·5° C with a homoeothermic blanket and rectal thermistor. Left and right cephalic veins and the trachea were cannulated. Immobilization of the eyes was accomplished with an initial 40 mg gallamine triethiodide (Flaxedil, May and Baker) intravenously, followed by continuous intravenous infusion in saline at 7–10 mg/kg.hr, in addition to bilateral cervical sympathectomy. Animals were moderately hyperventilated (35–40 ml. at 28/min). Spinal suspension was performed in some animals to reduce cortical pulsation and fine eye movements (Rodeick, Pettigrew, Bishop & Nikara, 1967). Blood pressure was monitored continuously with a Devices/CEC pressure transducer, via a cannula in the left carotid artery.

The bipolar e.e.g. was recorded throughout (bandpass 0·2–50 Hz), both before and after paralysis, between electrodes over the left primary visual cortex (Horseley-Clarke P2, LL2) and left auditory cortex, with a reference under the left temporalis muscle. For three of the acute preparations maintained on N_2O/O_2 these electrodes (extradural, 30-gauge, Teflon-insulated stainless-steel wires sealed into small craniotomies with Simplex acrylic dental cement) had previously been implanted under Nembutal anaesthesia. For the remainder, the electrodes consisted of small, self-tap stainless-steel screws, the blunt tip of the thread lying flush with the exposed dura.

Control e.e.g.s for both waking and drowsy states were established from the three chronically implanted animals a few days after recovery. These were easily distinguishable both in relative amplitude and component frequency. In the acute, paralysed preparations the e.e.g. and blood pressure were assessed jointly as an indication of anaesthetic adequacy. Anaesthetic depth was judged to be satisfactory in all cases involving N_2O/O_2 anaesthesia supplemented with neuroleptanalgesia or halothane. Using these e.e.g. criteria in preparation N_2O/O_2 alone was never found to be satisfactory in long-term experiments (E.F. Evans & P. Hammond, in preparation).

Animals were mounted stereotaxically, a small craniotomy performed over the right primary visual cortex, and the dura reflected immediately before the introduction of micropipettes. The exposure was subsequently sealed with 2% (w/v) I.D. Agar (Oxoid) at 39° C.

Pupils were dilated with 1% atropine sulphate, and the eyelids and nictitating membranes retracted with 10% phenylephrine hydrochloride. The eyes were protected with two-curve, neutral contact lenses. Correction lenses, selected by retinoscopy, focused the eyes on a matt white, translucent screen at a distance of 56·7 in. Locations of each optic disk and area centralis were determined by back projection onto the screen with an ophthalmoscope and cube corner prism.

Recording. Extracellular spike recordings were made from single cells in the striate cortex with low-impedance 4 M-NaCl micropipettes (tip diameter 1·5–2·5 μ). Units were recorded during nine successful vertical penetrations between Horseley–Clarke P2–P4·5 and RL 1·4–RL 2·5. Spikes were initially biphasic, negative-positive; all units described were isolated within the superficial 2 mm of striate grey matter. Some electrode tracks were confirmed histologically from 20 μ sections stained either with thionine, or with luxol fast blue and cresyl violet.

Signals were fed by a FET input-stage preamplifier (Narth, 1969) to an Isleworth A101 pre-amplifier (bandpass 0·2–5 kHz), and displayed conventionally on a

Tektronix RM 565 oscilloscope. Discriminated spikes were monitored aurally, fed to a gated electronic counter, to a variable time constant ratemeter, and to a Nuclear Chicago 7100 Data Retrieval Computer for on-line analysis of post-stimulus time histograms (PSTs). Raw data was stored on F/M magnetic tape for subsequent analysis.

Visual stimuli. The two identical projection assemblies used have been described in detail earlier (Andrews & Hammond, 1970*a*). Briefly, stimuli in slide form – monochromatic spots or slits, dark bars or edges set against monochromatic backgrounds – were projected onto the translucent screen. The screen was diffusely illuminated with white light derived from a tungsten source. Adaptation levels were measured with an S.E.I. photometer. Stimulus intensities could be reduced by interposing neutral density filters in nominal steps of 0·1 log units. Interference and N.D. filters were calibrated for relative quantum flux for each wave-length.

Flash presentations, photocell-monitored, were controlled by an electromechanical shutter. Fine control of stimulus position along mutually perpendicular axes was accomplished by a pair of pivoted mirrors mounted on a platform in front of each projector lens. Rotation of each mirror was controlled by a linear vibration generator; stimulus position was monitored on an $X-Y$ plotter. Receptive fields were mapped either on the $X-Y$ plotter or on the back of the screen.

Stimulus movement, 12° excursions in directions 180° apart, was generated by applying linear double-ramps (positive slope, followed after a variable pause by negative slope) to the appropriate vibration generator, this constituting one stimulus cycle. Cycle frequency could be varied. Stimulus half-cycles were obtained with an appropriately synchronized shutter. Stimulus velocity and excursion could be varied. Orientation of movement was adjusted by rotation of the mirror platform about the axis of the projector lens. Orientation of stimuli were controlled independently by rotation of the slide carrier.

RESULTS

Recordings were made from single cells in the right primary visual cortex, whose receptive fields were situated in or near the area centralis. Individual cells were held for up to 6 hr in order to assess their responses to monochromatic stimulation at each of three adaptation levels. Adaptation levels of -1, 0 and $+1$ log cd/m^2 were selected, corresponding to scotopic, to low or to high mesopic adaptation (Daw & Pearlman, 1969; Andrews & Hammond, 1970*a*, *b*; P. Hammond, in preparation). Following each log unit change in background luminance a time interval was allowed for adaptation to settle down to a steady level before making further recordings. This interval was a minimum of 10 min for a log unit increase, and a minimum of 30 min for a log unit decrease, in background luminance.

For each unit the analysis was confined to the receptive field for the dominant eye; the non-dominant eye was occluded. Axis orientation was determined and measured in degrees clock-wise from the vertical, the convention used by Pettigrew, Niakara & Bishop (1968*a*). Where possible, receptive fields were mapped with static flash presentations – small spots or appropriately orientated slits of 525 nm monochromatic light – at each

of the three adaptation levels. Many fields could not be mapped in this way.

For all units the optimal moving stimulus – an edge, a slit or dark bar of a certain width, orientated parallel with the axis and longer than the height of the receptive field – was determined. Then for each unit at each adaptation level a rectangular area of the receptive field was measured, defined by Barlow and others as the minimum response field (Barlow, Blakemore & Pettigrew, 1967). Primary borders of each receptive field parallel to the axis were measured either on the $X-Y$ plotter or from the averaged PSTs for twenty or fifty consecutive responses to movement of the optimal stimulus, thus defining the field width. Lateral borders of the field perpendicular to the axis were also determined, giving the receptive field height.

The results presented are for thirty-eight cells from a larger number isolated, for which data collection was complete or nearly so. The remainder either were not held long enough, or the specific trigger features were not successfully identified. Applying the classification of Hubel & Wiesel (1962) this sample contained more simple than complex units. There was also a preponderance of units with ipsilateral eye dominance. However, in each of the two subsections below, both simple and complex units, and units with ipsilateral and contralateral eye dominance, were well represented. Overall there was a noticeable preference for units with vertical, horizontal or 45°-diagonal axes. In particular, in agreement with Pettigrew *et al.* (1968*a*), directionally selective simple units possessed very low spontaneous frequencies (Fig. 1) and axes were usually near to vertical or horizontal orientations. The width of a minimum response field was often greater than its height, and was commonly greater than the receptive field width determined with static flashed presentations. The latter discrepancy was particularly marked for complex fields, and to some extent must be due to the width of a moving target.

As in earlier reports (Andrews & Hammond, 1970*a*, *b*), intensities of monochromatic stimuli are expressed either in terms of relative quantum flux between different wave-lengths, or as quantum flux relative to threshold.

Chromatic sensitivity and spatial organization of receptive fields

In the first series of experiments optimal stimuli, appropriately orientated, were moved back and forth across each receptive field perpendicular to the axis, with a linear velocity of 12·8°/sec and a total excursion of 12°. The stimulus cycle was repeated at 2·5 sec intervals, the second half-cycle commencing 1·1 sec after the first. At each of eleven wave-lengths from 400 to 650 nm in order, responses to twenty consecutive

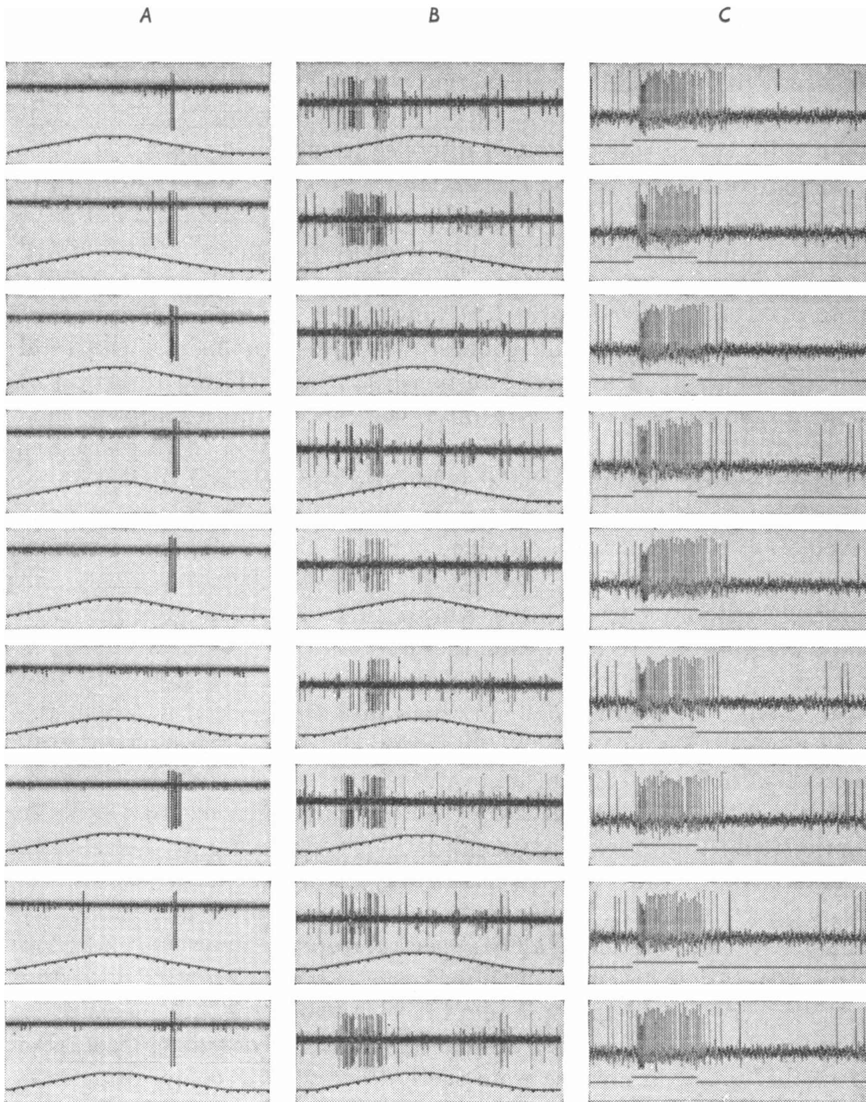

Fig. 1. Trains of responses to consecutive identical monochromatic stimuli for a directionally selective simple cortical unit (*A*) and for a complex unit with a bimodal response to movement and a marked directional preference (*B*); each column is a continuous record. Note the large variability of cortical unit responses compared with that for units from the optic tract (*C*), and an absence of spontaneous firing in the case of the simple cell. For the cortical units optimally orientated slits were moved back and forth across the receptive field with a velocity of 12·8°/sec and a total excursion of 12° in each direction (lower trace of each record). This cycle was repeated at intervals of 2·5 sec. Time pips on lower trace: 100 msec. Slit width: 1° in *A*, 4° in *B*. Stimulus in *C*: 1° spot centred over receptive field and presented as a 300 msec flash every 1·3 sec. Adaptation level: 0 log cd/m² throughout. Stimulus wave-length: 501 nm; approximately 1 log unit suprathreshold in each case.

stimulus cycles were recorded. Stimuli of different wave-length were equated for quantum flux, and related to threshold at the wave-length of peak sensitivity prevailing under the particular level of background luminance in use at the time.

Some units gave a unidirectional response to movement (e.g. Fig. 1*A*); more usually responses were bidirectional with a more or less marked preference for one direction (e.g. Fig. 1*B*). Analysis was usually limited to responses to the preferred direction of movement. Spikes, discriminated from the raw data, were counted electronically for each of the twenty responses at each wave-length. The mean and S.D. of each group of responses was computed. The counter was gated to include the total number of spikes in a unimodal response to the preferred direction of movement; for bimodal responses (often correlated with a receptive field with an inhibitory centre stripe and excitatory side bands) each phase was counted separately. The mean values obtained were plotted against wave-length to give a spectral response curve for movement. For most units reported such functions were obtained for two or for all three levels of adaptation.

Spectral response curves for a simple unit, for both low and high mesopic adaptation, are illustrated in Fig. 2 and show a clear change in colour sensitivity. The evidence of a Purkinje shift was for every unit consistent with input from 556 nm cones and 500 nm rods, though the shift was sometimes not as obvious as for the unit of Fig. 2. Spectral response functions for cortical units were never as clear-cut as the comparable functions for static flashed presentations obtained from units in the optic tract (Andrews & Hammond, 1970*b*; and see Fig. 3). The reasons for this are considered below. Qualitatively, however, the results reflect those at the retinal level. Under scotopic conditions chromatic sensitivity was indicative of rod function alone. Spectral response functions under low mesopic adaptation indicated predominance of rod activity (Fig. 2; Fig. 3*A*, *B*). Conversely, high mesopic adaptation favoured the cone mechanism, with residual interaction from the partially saturated rods (Fig. 2). For bidirectional units, in no case were there differences in colour sensitivity for the two directions of movement. No conclusive evidence was obtained for input involving 450 nm cones (Pearlman & Daw, 1970), additional to the more common 556 nm cone mechanism.

One of the greatest problems encountered was the sometimes enormous variability between consecutive responses to stimuli identical in every respect (Fig. 1*A*, *B*). One stimulus might be almost totally ineffective whereas the next would evoke a brisk response. Even averaging twenty responses gave a mean spike count with a relatively high S.D. (Fig. 3*A*). With light anaesthesia induced by N_2O/O_2, desirable for recording neural

activity at higher levels, it has been shown that residual eye movements of up to 2° are still present under Flaxedil paralysis (Rodeick *et al.* 1967). These are reduced to 0·5° or less following bilateral cervical sympathectomy (the technique used here). For a number of reasons it seems unlikely that such eye movements can account for the observed response variability

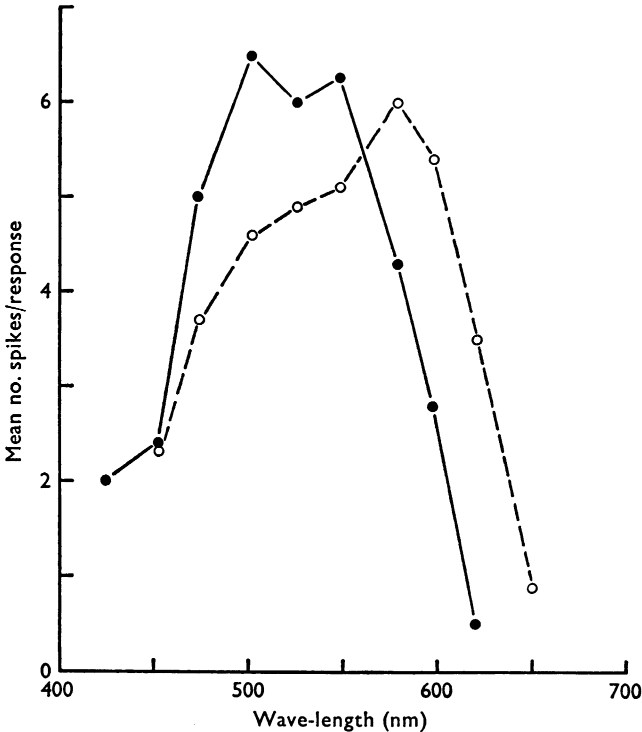

Fig. 2. Purkinje shift for a simple cortical cell as revealed by spectral response functions for the preferred direction of movement under two different levels of adaptation: high mesopic adaptation (1 log cd/m^2, open circles and dashed line), low mesopic adaptation (0 log cd/m^2, filled circles and continuous line). Stimuli were 4°-wide monochromatic slits of different wave-length but identical quantum flux, moved across the receptive field with a linear velocity of 12·8°/sec. Each point is the mean of twenty consecutive responses at a specific wave-length.

from monocular fields, though they are of critical importance for binocular work. Here, stimulus excursions (12°) were substantially greater than the widest receptive fields encountered. Repeated careful ophthalmoscopic observation of retinal landmarks failed to reveal movement. For retinal work Nembutal anaesthesia coupled with Flaxedil paralysis had resulted in extremely good stability of eye position, even without sympathectomy (Rodeick *et al.* 1967; Andrews & Hammond, 1970*a*). In the present cortical

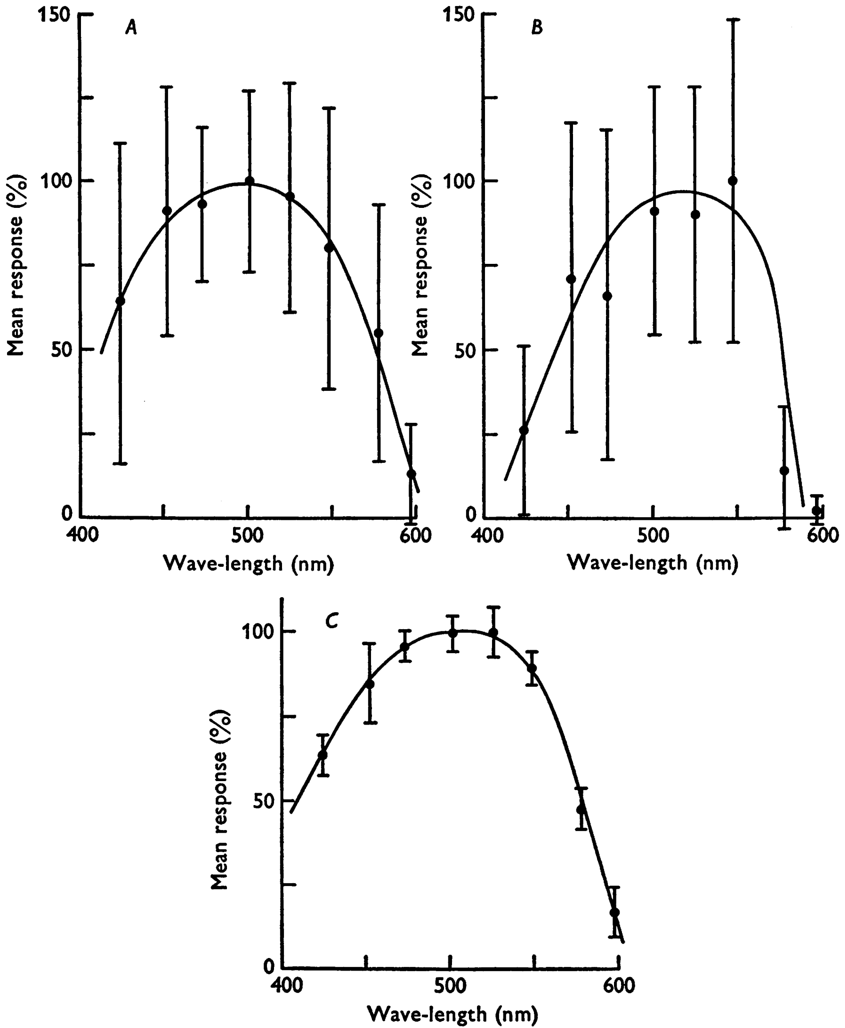

Fig. 3. Comparison of spectral response curves for two directionally selective simple cortical cells and one optic tract fibre. *A*: simple cell, neuroleptanaesthesia under 50 %/50 % N_2O/O_2, droperidol and phenoperidine. *B*: simple cell, Nembutal anaesthesia. *C*: optic tract fibre, Nembutal anaesthesia. Note in particular that response variability for cortical units is substantially greater than for retinal units (see text). Each function is for low mesopic adaptation (0 log cd/m^2), peak 500 nm, rod function predominant; stimuli are all of identical quantum flux, approximately 1 log unit suprathreshold at the wave-length of peak sensitivity in each case. The three units illustrated were selected for similarity of response magnitude in terms of numbers of spikes. Each point gives the mean number of spikes in twenty consecutive responses to stimulation at a given wave-length, converted to percentage for strict comparison between units; limits given are $\pm$ 1 S.D. of the mean.

series one preparation was deliberately studied under Nembutal and Flaxedil for comparison. Variability of cortical unit responses was not significantly different from that for the N_2O/O_2 preparations, but still very substantially greater than for retinal units (Fig. 3). The only systematic differences seen under Nembutal anaesthesia, compared with N_2O/O_2 anaesthesia, were a general reduction in responsiveness of units and depression of spontaneous frequencies. Thus in the lightly anaesthetized, as in the unanaesthetized preparation, variability would seem to be an inherent feature of cortical units, presumably a function of ongoing activity and influence from other centres. In this respect the frequently clustered firing of cortical cells does not help. Their responsiveness is profoundly influenced by the immediately preceding pattern of spontaneous or evoked activity; suppression resulting from a spontaneous burst or evoked response may last for at least several hundred milliseconds, and possibly longer (unpublished observations). In context it was not unexpected that, following a response weaker than average in a train, the subsequent stimulus would frequently evoke a particularly vigorous discharge (see Fig. 1*A*, *B*).

Despite the universality of the Purkinje shift, conclusive evidence for a corresponding change in receptive field organization was obtained for only one unit. This was a simple unit with contralateral eye dominance and an axis orientation of 90° (horizontal). Under scotopic or low mesopic adaptation field-mapping with a static 0·5° slit of the same orientation revealed a central 2·5° excitatory stripe, with upper and lower inhibitory flanks respectively 0·8° and 2° wide. For high mesopic adaptation the upper inhibitory flank was totally undetectable (Fig. 4*A*). Averaged PSTs for responses to movement of the identical stimulus showed a comparable change (Fig. 4*B*). Responses to movement were monophasic and bidirectional, with a marked preference for upward movement. Due to loss of the upper inhibitory flank, with increase in adaptation level the response terminated progressively later for the preferred direction, and commenced progressively earlier for downward movement; the directional preference became even more marked. Thus under high mesopic adaptation, although the upper primary border of the minimum response field was placed higher than at lower adaptation levels, for the receptive field plot the upper limit was actually lower in the visual field. Though the results are here consistent with an upper inhibitory flank mediated exclusively by input from rods, they highlight an apparent discrepancy in spatial organization defined respectively by a static field map or a minimum response field.

For the receptive fields of all other units, changes in spatial organization were at best only marginal. Again response variability precluded accurate

measurement. An additional difficulty was the possible ambiguity between response latency and spatial change. Variation of response latency as a function of stimulus intensity is well established. Furthermore, it is known from retinal work that cone-induced responses are of substantially shorter latency than those mediated by rods (Gouras & Link, 1966; Gouras, 1967,

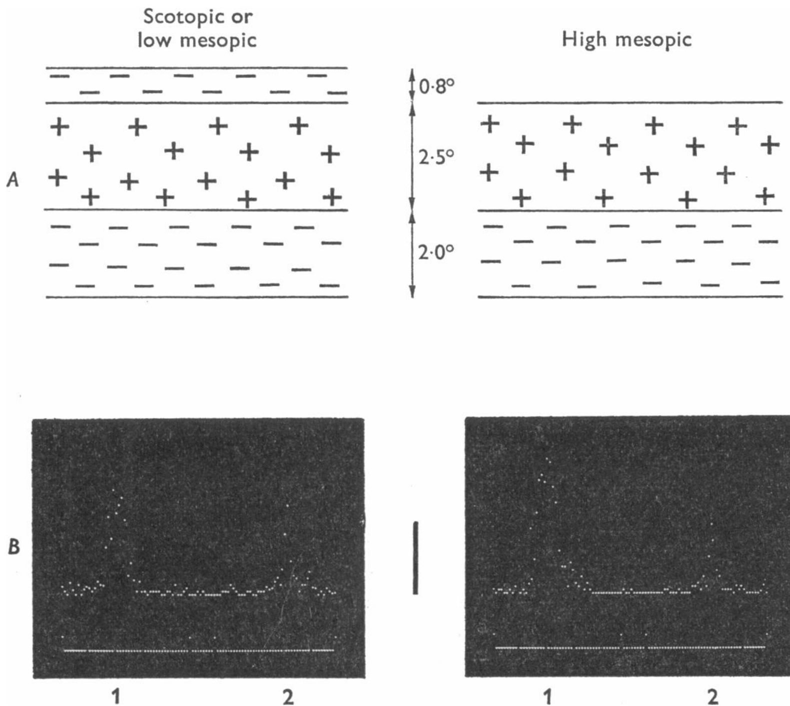

Fig. 4. Change in receptive field organization and responsiveness of a simple cortical cell, related to input mediated by rods and cones. *A*: receptive field map; *B*: averaged PSTs for twenty consecutive responses to movement. [Detail for *B* – *stimulus*: 525 nm monochromatic slit orientated parallel to the field axis; width 0·5°; intensity approximately 1 log unit suprathreshold in each case; velocity 12·8°/sec; 12° excursion; upward movement (1) followed by downward movement (2). *PSTs*: 2 sec sweep, 20 msec/bin; vertical bar calibration 20 spikes/bin; the four pips on the lower trace of the PSTs mark in order the beginning and end of upward and downward movement respectively.]

1968; Hammond, 1968; Andrews & Hammond, 1970*a*, *b*). Consequently with change from mesopic to scotopic adaptation a shift in the centre of gravity of a minimum response field in the same direction as the movement of the stimulus was quite often noticed, with no corresponding change in the minimum response field width. Such variations acquire greater significance for stimuli moved with high velocity, compared with latency

changes which are explicitly due to spatial reorganization of a receptive field. Of necessity, a relatively high movement velocity of 12·8°/sec was used for these experiments, to minimize the analysis time for each unit. Thus, to take an example, it was sometimes not easy to decide whether an increase in the latency of a response to movement was due to the inherent latency of cone or rod responses *per se*, or to a genuine shift in a receptive field border.

Increment threshold sensitivity and spatial organization of receptive fields

For the second series of experiments stimulus velocity was reduced to 1·5°/sec so that latency changes due to stimulus intensity, or to preferential involvement of cone or rod mechanisms, would be negligible compared with those due to any spatial change in the organization of a receptive field. Stimulus half-cycles, in the preferred direction for each unit, were used to obviate possible interaction with responses to the opposite direction of movement. The repeat frequency was reduced to one presentation every 5 sec to minimize interaction between consecutive responses. Excursion was reduced to 6° to decrease the time for data collection whilst maintaining minimal interaction between stimuli.

Wave-lengths 452 and 578 nm were selected from the eleven wave-lengths previously used. These wave-lengths were chosen since near threshold, in the absence of 450 nm-cone input, they would give preferential activation of the 500 nm-rod and 556 nm-cone mechanisms respectively. Stimulus trains were frequently increased from twenty to fifty for each specific stimulus, to average out some of the response variability. Spikes in each train of responses were counted for a unimodal response, or for each mode of a biphasic response, to the preferred direction of movement; means and standard deviations were computed as before. At each adaptation level the threshold, based on twenty or fifty responses, was determined for each wave-length. Trains of responses at nominal successive steps of 0·3 log units above threshold were recorded for each wave-length and subsequently analysed.

Although the rod absorption maximum for cat probably lies in the region of 500 nm, it has been shown in an earlier paper that the scotopic sensitivity maximum is placed at about 507 nm, the discrepancy possibly being due to intra-ocular absorption and tapetal reflectivity (Andrews & Hammond, 1970*a*). For retinal units the scotopic and photopic spectral sensitivity curves could thus be fitted reasonably by the nomogram curves (Dartnall, 1953) for visual pigments 507 and 556 respectively. If only one type of rods (peak 507 nm) and one type of cones (peak 556 nm) are involved in the Purkinje shift, the Dartnall functions predict that threshold

will be 0·44 log units lower at 452 nm than at 578 nm for dark-adaptation, and 0·52 log units higher for light-adaptation. Thus the total changeover from cone to rod vision should involve a relative shift in threshold for these wave-lengths of the order of 0·96 log units.

Actual measurements from six cortical units showed that the mean threshold at 452 nm was 0·43 log units lower than at 578 nm (range 0·33–0·69) for scotopic adaptation (-1 log cd/m^2); for high mesopic adaptation (1 log cd/m^2), at which there is a substantial degree of rod saturation, mean threshold at 452 nm was 0·53 log units higher than at 578 nm (range 0·21–0·77). The mean relative shift in threshold for the same units was 1·00 log units (0·91–1·10). For the comparatively small number of units sampled the closeness of agreement between the theoretical predictions and the experimental observations is somewhat fortuitous, but the implications are clear. Obviously the absolute range for mesopic interaction varies considerably from unit to unit, but the magnitude of the relative shift in threshold is remarkably constant. The result is consistent with the earlier observations and indicates that every unit receives input mediated by each of only two receptor mechanisms, i.e. dual input from 556 nm cones and 500 nm rods.

With the use of slow movement velocity to avoid confusion between response latency and spatial information, from averaged PSTs to movement it was possible to measure the position of each primary border of a minimum response field to an accuracy of 0·1° or better. Yet although the Purkinje shift was well-defined for every unit, at or above threshold there was still no evidence of any spatial change in receptive field organization with change in background luminance. It is concluded that whilst cortical units receive information mediated both by cones and rods, for the great majority of units the spatial distribution of these inputs is effectively identical.

DISCUSSION

All visual cortical cells so far examined in cat exhibit a Purkinje shift comparable to that for retinal units (Andrews & Hammond, 1970*a*, *b*), and for most geniculate units (Daw & Pearlman, 1969; Pearlman & Daw, 1970). Yet it is somewhat perplexing to find that spatial reorganization of receptive fields between light and dark adaptation, *vis-à-vis* cones and rods, so well evidenced at the retinal level (Andrews & Hammond, 1970*b*), is reflected little if at all in the cortex. The absence of such difference, one of several prerequisites for cone-rod opponency and a possible basis for behavioural colour discrimination, would suggest that the cortex is not concerned with colour analysis in the mesopic range.

Undoubtedly the cat to some extent also possesses the behavioural ability to make colour discriminations in the photopic range, even when the rods are fully saturated (Pearlman & Daw, 1970). But equally it seems that the cortex may not be involved. There is no evidence at all that cortical units receive cone-cone opponent input, or even input from a single class of cones other than those with maximum sensitivity at 556 nm. In view of the rarity of opponent units in LGN with 450 nm cone input in addition to that from 556 nm cones—three cells of 108 in a recent survey by Pearlman & Daw (1970), no cells in an earlier study (Daw & Pearlman, 1969)—there is the possibility that the cortical sample described here is too small to have included any cells with 450 nm input. This seems unlikely, however, for a cell sample whose receptive fields are related specifically to retinal areas subserving central vision and of high cone density, usually associated with colour discrimination.

In many ways there is a close parallel with the primate visual system. For monkey, the lateral geniculate is particularly favourably organized with respect to colour (De Valois, Smith, Kitai & Karoly, 1958; De Valois, 1965; De Valois, Abramov & Jacobs, 1966; Wiesel & Hubel, 1966; De Valois, Abramov & Mead, 1967). The great majority of cells show cone–cone opponency, with or without the antagonistic centre-surround organization, and there are several subgroups within each of these categories. Some cells in the retina are comparably organized for colour (Hubel & Wiesel, 1960). In the cortex, on the other hand, again from the area for central vision, colour information is very poorly represented; only a small proportion of cells are colour-coded (Hubel & Wiesel, 1968).

The implication is that for cat and possibly primates the cortex, at least the primary area, is not fundamentally organized for colour, but rather for discrimination of form, orientation and movement (Hubel & Wiesel, 1962, 1968; Campbell, Cleland, Cooper & Enroth-Cugell, 1968; Pettigrew *et al.* 1968*a*), binocular interaction and stereopsis (Hubel & Wiesel, 1962, 1968; Barlow *et al.* 1967; Nikara, Bishop & Pettigrew, 1968; Pettigrew, Nikara & Bishop, 1968*b*; Blakemore, 1970). In cat the existence of dual input from cones and rods may impart nothing more to cortical units than an extension of their functional range. It is quite plausible that wave-length discrimination may rest primarily within the lateral geniculate nucleus, rather than in cortex, and single unit recordings to date would favour this notion. There is of course the alternative that cortical colour information may be substantial, but that with the addition of a colour variable to an already highly complicated organization, the organization for many cells becomes such as to have eluded analysis.

There still remains the question of why spatial reorganization for cone and rod receptive fields of retinal units is not detectable in the cortex,

particularly since the retinal results are in line with the change of acuity with adaptation which can be observed in psychophysical experiments. The summary diagram of Fig. 5 is intended to be cross-referenced with the argument developed in the following paragraphs. The obvious possibility is that the retinal input is spatially reorganized in the LGN, so that the relevant information is filtered out before reaching the cortex. Recent work on LGN indicates that receptive fields of on-centre and off-centre geniculate units do not merely mirror those of the comparable fibre types in the optic tract. Each type of geniculate cell receives input from both

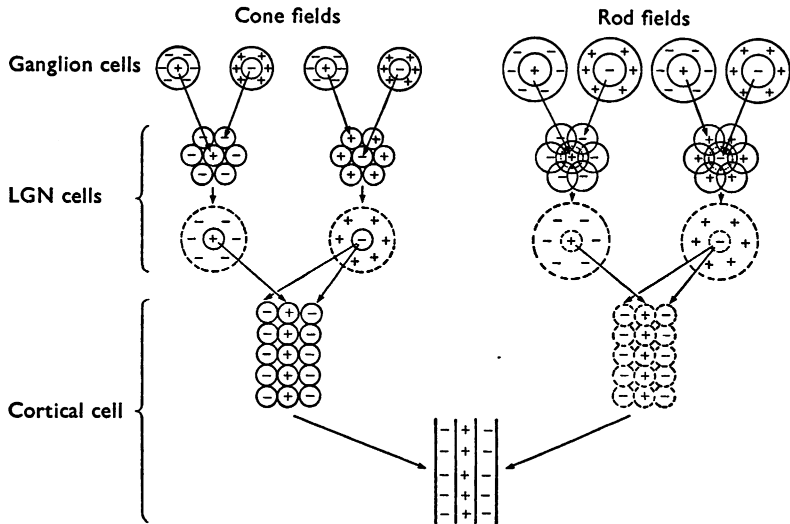

Fig. 5. Schematic illustration of a theory for the build-up of cortical fields, based on the known properties of retinal and geniculate fields, to explain why in general cortical units exhibit a Purkinje shift in the absence of any spatial reorganization of their receptive fields. Effectively the cortical field is structured only from geniculate field centres; the geniculate fields are in turn basically composed from retinal field-centres. The cortical field depicted in the lowest line has been chosen as a typical example, though the scheme is equally applicable to all types of cortical field. For details see text.

on-centre and off-centre optic tract fibres. An on-centre geniculate neurone receives field-centre input from an on-centre optic tract fibre, and surround input from a number of off-centre fibres. Similarly, a geniculate off-centre unit receives centre input from one off-centre fibre and surround input from several on-centre fibres (Singer & Creutzfeldt, 1970). In other words, the component parts of geniculate fields are essentially constructed from retinal field-centres. At the retinal level the diameter of a receptive

field centre is small compared with its surround. Thus in the geniculate it is to be expected that for a changeover from cone fields to rod fields associated with the level of adaptation, enlargement of the receptive field overall will be small compared with that for a retinal cell. Change in centre and surround diameter will both be small, comparable to the change in field-centre diameter for a retinal cell.

For fibres in the optic tract field-centres can be less than 0·25° in diameter, and there is a tendency for fields placed near the area of central vision to possess smaller centres than those situated more peripherally (Andrews & Hammond, 1970*a*). Taking this figure for the cone field-centre diameter, then on the assumption that the diameter for the rod field-centre is twice as large (Andrews & Hammond, 1970*b*) the overall change in diameter for a centrally placed geniculate field would be of the order of 0·25°. The prediction for the geniculate field-centre is less certain, for the field is built up from antagonistic field-centres in juxtaposition. Certainly one might expect the change in centre diameter to be small compared with the surround, since the antagonism between centre and surround for geniculate units is greater than for retinal ganglion cells (Hubel & Wiesel, 1961). On the other hand, when the cone field-centres of the fibre input are operant, it must be assumed that there are no holes in the geniculate unit receptive field. Since the cone and rod field-centres of the fibre input have identical loci, under scotopic conditions there must be substantial overlap between the antagonistic rod field-centre inputs, and there is no reason why these individually should have unequal influence on the geniculate cell. It follows that there is a balanced annular zone of overlap between the geniculate rod field-centre and rod field-surround. Thus it is very probable that there will be no change at all at the centre. The result is simply a geniculate field of identical centre size, but with loss of definition at the centre-surround boundary.

Hubel & Wiesel (1962) have proposed a model for the synthesis of cortical fields from geniculate fields. They suggested that cortical cell fields with a central excitatory or inhibitory stripe and symmetrical antagonistic flanks might be built up from a row of either on-centre or off-centre geniculate cells. For fields where the flanks were asymmetrically distributed they supposed that the dominant flank might be 'reinforced' by the appropriate class of geniculate cells. If this hypothesis is correct, then for such cortical cells from the area of central vision the present work should have detected a change in the width of receptive field maps or minimum response fields of the order of 0·25°, a magnitude comparable to that predicted above for the change in overall diameter of geniculate receptive fields. The absence of any such change is consistent with the predictions for geniculate field-centre organization and would indicate

that the emphasis placed by Hubel & Wiesel on reinforcement is too low. The result suggests that reinforcement obtains more universally than envisaged in their model, and that relatively the geniculate field surrounds are unimportant; this is more in line with their theory that a cortical field with adjacent excitatory and inhibitory stripes receives input from neighbouring rows of on-centre and off-centre geniculate cells.

In conclusion it seems that the picture is really such that a cortical cell field is based substantially only on the convergent input from field-centres of geniculate cells, just as the geniculate cell fields are basically composed from retinal cell field-centres. It is proposed that this selectivity at each level of the visual pathway, for field-centres from an earlier level, may constitute a multi-stage sharpening in the visual process.

Specific thanks are due to A. Jones and R. P. Kempson for invaluable technical assistance, and to Miss J. E. Cave for her painstaking work in preparation of this manuscript. I also wish to acknowledge the interest shown by Denis Andrews.

REFERENCES

ANDREWS, D. P. & HAMMOND, P. (1970*a*). Mesopic increment threshold spectral sensitivity of single optic tract fibres in the cat: cone-rod interaction. *J. Physiol.* **209**, 65–81.

ANDREWS, D. P. & HAMMOND, P. (1970*b*). Suprathreshold spectral properties of single optic tract fibres in cat, under mesopic adaptation: cone-rod interaction. *J. Physiol.* **209**, 83–103.

BARLOW, H. B., BLAKEMORE, C. & PETTIGREW, J. D. (1967). The neural mechanism of binocular depth discrimination. *J. Physiol.* **193**, 327–342.

BARLOW, H. B., FITZHUGH, R. & KUFFLER, S. W. (1957*a*). Dark-adaptation, absolute threshold and Purkinje shift in single units of the cat's retina. *J. Physiol.* **137**, 327–337.

BARLOW, H. B., FITZHUGH, R. & KUFFLER, S. W. (1957*b*). Change of organization in the receptive fields of the cat's retina during dark-adaptation. *J. Physiol.* **137**, 338–354.

BLAKEMORE, C. (1970). The representation of three-dimensional visual space in the cat's striate cortex. *J. Physiol.* **209**, 155–178.

CAMPBELL, F. W., CLELAND, B. G., COOPER, G. F. & ENROTH-CUGELL, CHRISTINA (1968). The angular selectivity of visual cortical cells to moving gratings. *J. Physiol.* **198**, 237–250.

DARTNALL, H. J. A. (1953). The interpretation of spectral sensitivity curves. *Br. med. Bull.* **9**, 24–30.

DAW, N. W. & PEARLMAN, A. L. (1969). Cat colour vision: one cone process or several? *J. Physiol.* **201**, 745–764.

DE VALOIS, R. L. (1965). Analysis and coding of colour vision in the primate visual system. *Cold Spring Harb. Symp. quant. Biol.* **30**, 567–579.

DE VALOIS, R. L., ABRAMOV, I. & JACOBS, G. H. (1966). Analysis of response patterns of LGN cells. *J. opt. Soc. Am.* **56**, 966–977.

DE VALOIS, R. L., ABRAMOV, I. & MEAD, W. R. (1967). Single cell analysis of wavelength discrimination at the lateral geniculate nucleus in the macaque. *J. Neurophysiol.* **30**, 415–433.

De Valois, R. L., Smith, C. J., Kitai, S. T. & Karoly, A. J. (1958). Response of single cells in monkey lateral geniculate nucleus to monochromatic light. *Science, N.Y.* **127**, 238–239.

Gouras, P. (1967). The effects of light adaptation on rod and cone receptive field organization of monkey ganglion cells. *J. Physiol.* **192**, 747–760.

Gouras, P. (1968). Identification of cone mechanisms in monkey ganglion cells. *J. Physiol.* **199**, 533–547.

Gouras, P. & Link, Krista (1966). Rod and cone interaction in dark-adapted monkey ganglion cells. *J. Physiol.* **184**, 499–510.

Granit, R. (1943). The spectral properties of the visual receptors of the cat. *Acta physiol. scand.* **5**, 219–229.

Granit, R. (1945). The colour receptors of the mammalian retina. *J. Neurophysiol.* **8**, 195–310.

Granit, R. (1955). *Receptors and Sensory Perception.* New Haven: Yale University Press.

Gunter, R. (1952). The spectral sensitivity of dark-adapted cats. *J. Physiol.* **118**, 395–404.

Gunter, R. (1954). The spectral sensitivity of light-adapted cats. *J. Physiol.* **123**, 409–415.

Hammond, P. (1968). Spectral properties of dark-adapted retinal ganglion cells in the plaice (*Pleuronectes platessa* L.). *J. Physiol.* **195**, 535–556.

Hubel, D. H. & Wiesel, T. N. (1960). Receptive fields of optic nerve fibres in the spider monkey. *J. Physiol.* **154**, 572–580.

Hubel, D. H. & Wiesel, T. N. (1961). Integrative action in the cat's lateral geniculate body. *J. Physiol.* **155**, 385–398.

Hubel, D. H. & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *J. Physiol.* **160**, 106–154.

Hubel, D. H. & Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *J. Physiol.* **195**, 215–243.

Kuffler, S. W. (1953). Discharge patterns and functional organization of mammalian retina. *J. Neurophysiol.* **16**, 37–68.

Mello, N. K. & Peterson, N. J. (1964). Behavioural evidence for colour discrimination in cat. *J. Neurophysiol.* **27**, 323–333.

Meyer, D. R. & Anderson, R. A. (1965). Colour discrimination in cats. In *Colour Vision*, ed. de Reuck, A. V. S. & Knight, Julie, pp. 325–339. Boston: Little Brown.

Narth, C. S. (1969). An inexpensive field effect transistor preamplifier for use with extracellular micro-electrodes. *J. Physiol.* **200**, 102–103*P*.

Nikara, T., Bishop, P. O. & Pettigrew, J. D. (1968). Analysis of retinal correspondence by studying receptive fields of binocular single units in cat striate cortex. *Expl Brain Res.* **6**, 353–372.

Pearlman, A. L. & Daw, N. W. (1970). Opponent colour cells in the cat lateral geniculate nucleus. *Science, N.Y.* **167**, 84–86.

Pettigrew, J. D., Nikara, T. & Bishop, P. O. (1968*a*). Responses to moving slits by single units in cat striate cortex. *Expl Brain Res.* **6**, 373–390.

Pettigrew, J. D., Nikara, T. & Bishop, P. O. (1968*b*). Binocular interaction on single units in cat striate cortex: Simultaneous stimulation by single moving slit with receptive fields in correspondence. *Expl Brain Res.* **6**, 391–410.

Rodeick, R. W., Pettigrew, J. D., Bishop, P. O. & Nikara, T. (1967). Residual eye movements in receptive field studies of paralysed cats. *Vision Res.* **7**, 107–110.

Sechzer, J. A. & Brown, J. L. (1964). Colour discrimination in the cat. *Science, N.Y.* **144**, 427–429.

Singer, W. & Creutzfeldt, O. D. (1970). Reciprocal lateral inhibition of on- and off-centre neurones in the lateral geniculate body of the cat. *Expl Brain Res.* **10**, 311–330.

Weale, R. A. (1953). Photochemical reactions in the living cat's retina. *J. Physiol.* **122**, 322–331.

Wiesel, T. N. & Hubel, D. H. (1966). Spatial and chromatic interactions in the lateral geniculate body of the rhesus monkey. *J. Neurophysiol.* **29**, 1115–1156.