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THE AFFERENT CONNEXIONS AND LAMINAR DISTRIBUTION OF CELLS IN AREA 18 OF THE CAT

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SUMMARY

1. The receptive field properties, laminar distribution and afferent connectivity of cells in area 18 of the cat are described.

2. Testing with both moving and stationary stimuli revealed three main receptive field types which have been termed S, C and B, respectively (cf. Henry, 1977; Henry, Lund & Harvey, 1978). All three classes may show end-zone inhibition and units exhibiting this property have been designated S_H, C_H and B_H.

3. S cells can be divided into spatially separate light and/or dark edge response regions when tested with moving edges and usually have separate ON and/or OFF areas when tested with stationary flashing stimuli. They are the most commonly encountered cell type in area 18 and occur most frequently in laminae IIIb, IVa and VI.

4. Both C and B cells have spatially coincident light and dark edge response regions and give mixed ON and OFF discharges when tested with stationary flashing stimuli. Compared to B cells however, C cells have large receptive fields, they are broadly tuned for stimulus orientation and generally have a relatively high rate of spontaneous activity. C cells are more common than B cells and are encountered most often in laminae IVb and V.

5. Electrical stimulation of the optic chiasm (OX) and optic radiation (OR) was used to examine the afferent connectivity of parastriate neurones. Cells driven from both OX and OR have been divided into two main groups and it is argued that group 1 cells are directly, and group 2 cells are indirectly, excited by rapidly conducting afferent fibres. Group 1 cells are found most often in laminae IIIb, IVa, IVb and VI, and their distribution closely follows the anatomically defined laminar disposition of geniculocortical afferent terminals. Group 2 neurones predominate in laminae II–IIIa, IIIa and V.

6. The majority of S and S_H cells are directly driven, whereas most C and C_H cells have OX and OR latencies suggestive of indirect activation by thalamic afferents.

7. The intrinsic organization and possible functional role of area 18 is discussed in the light of these results.

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INTRODUCTION

It is now widely agreed that much of the processing of visual information which occurs in area 18 of the cat is not dependent on the functional integrity of the striate cortex. As early as 1942, Talbot reported that the lateral visual area in the lateral gyrus responded independently of more medial parts of the cortex. More recently, both Dreher & Cottee (1975) and Sherk (1978) have shown that the response properties of single parastriate neurones remain, to a large extent, unaltered by inactivation of area 17. This independence arises from the fact that area 18 receives a substantial projection directly from the thalamus. The thalamocortical fibres innervating area 18 are of large diameter (Garey & Powell, 1971) and arise, in the main, from the larger cells within the dorsal lateral geniculate nucleus (d.l.g.n.) and medial interlaminar nucleus (m.i.n.) (Garey & Powell, 1967; Gilbert & Kelly, 1975; Garey & Blakemore, 1977; Hollander & Vanegas, 1977; LeVay & Ferster, 1977). The axons terminate mostly in lamina IV, to some extent in lamina VI and rarely in other layers (Garey & Powell, 1971; Rosenquist, Edwards & Palmer, 1974; LeVay & Gilbert, 1976). Thalamo-parastriate fibres are generally rapidly conducting (Toyama & Matsunami, 1968; Stone & Dreher, 1973; Tretter, Cynader & Singer, 1975) and most of the neurones in the d.l.g.n. and m.i.n. efferent to the parastriate cortex appear to be Y cells (Stone & Dreher, 1973; Kratz, Webb & Sherman, 1978; Dreher & Sefton, 1979).

Despite the fact that area 18 processes information largely in parallel with area 17, the parastriate cortex has not been as intensively studied, in either a qualitative or a quantitative sense, and there has been little attempt to relate the physiology to the morphology of the area. The present work describes the visual response properties of parastriate neurones with both centrally and peripherally located receptive fields and examines the laminar disposition of the various cell classes. Since area 18 receives predominantly large rather than small axons and since fast thalamic afferents are relatively easy to excite electrically from both the OR and OX (cf. Singer & Bedworth, 1973; Stone & Dreher, 1973; Tretter *et al.* 1975), it has proved possible to assess the synaptic connectivity of a large proportion of parastriate neurones. This information has been correlated with the visual properties and laminar locations of the cells, making it possible to put forward a tentative model which attempts to show how incoming visual signals are processed and elaborated within area 18. Some aspects of this work have been presented in a preliminary form elsewhere (Harvey, 1977; Harvey & Camarda, 1978).

METHODS

Cats (weight range 2·5–4·0 kg) were anaesthetized with a halothane (induced on 4%, maintained on 1–1·5%) and 70% N_2O/30% O_2 mixture during the surgical procedures. A tracheal and venous cannula were inserted. The animal's temperature was maintained at 38 °C by an electric heating blanket. Eye movements were reduced to a very low level by paralysis of the animal and bilateral cervical sympathectomy. Paralysis was induced by an initial I.V. injection of 40 mg gallamine triethiodide (Flaxedil; May & Baker) and was maintained by a continuous I.V. infusion of a mixture of Flaxedil (16·3 mg/hr), C-toxiferine I (toxiferine dichloride; Hoffmann La Roche; 1·0 mg/hr) and dextrose (J. T. Baker; 260 mg/hr) in a 0·9% saline solution (5·8 ml./

hr). After paralysis and during recording, cats were artificially respired, usually at a rate of 25 strokes per min, with a 70% N_2O/30% O_2 mixture. Stroke volume varied from 40 to 50 ml. per stroke according to the size of the animal.

In order to avoid disturbing the response properties of cortical neurones, the animal must be kept lightly anaesthetized. These properties are believed to be least disturbed when the anaesthetic agent is N_2O. There is evidence that, under similar post-operative conditions to those prevailing during the electrophysiological recordings in the present experiments, N_2O provides an adequate anaesthetic cover (Dubin & Cleland, 1977; cf. Venes, Collins & Taub, 1971). Throughout the present experiments, in addition to the N_2O anaesthesia, regular injections of a long-acting local anaesthetic (bupivacaine; Marcaine), administered at wound margins and pressure points, further reduced the possibility that the animal experienced pain. A topical antibiotic powder, Neosporin (Calmic Pharmaceuticals), was also infused into all wounds and fortified benethamine penicillin (Triplopen; Glaxovet; 0·2 ml.) and occasionally 2–5 mg hydrocortisyl (Roussel) were injected intramuscularly.

The corneas were protected with plastic contact lenses of zero power and the eyelids and nictitating membranes were retracted with neosynephrine (Winthrop; 2·5%). Drops of oxybuprocaine hydrochloride (Minims; Smith & Nephew Pharmaceuticals) and Neosporin ophthalmic solution (Calmic Pharmaceuticals) were placed on each eye and the pupils were dilated with a drop of atropine (Sigma; 1%). An indirect ophthalmoscope (Fundus Camera, Carl Zeiss, Oberkochen/Wuertt) was used for projecting retinal landmarks. None of the animals used in these experiments had any pathological disturbances in the retina, such as central retinal degeneration. Artificial pupils (3 mm in diameter) were centred on the area centralis using the modified viewing system of the Fundus camera (Bishop, Henry & Smith, 1971). A slit retinoscope (Hamblin) was used to refract the cat for a viewing distance of 1 m and appropriate spectacle lenses were placed in front of the artificial pupil. The blind spot and area centralis of each eye were plotted at intervals during the course of the experiment in order to monitor eye position.

During surgery, small craniotomies and durotomies were performed for the insertion of the recording and stimulating electrodes. For recording, a tungsten in glass micro-electrode (Levick, 1972) was placed just above the cortical surface. A recording chamber, previously cemented around the craniotomy was then sealed with agar and wax (Bishop *et al.* 1971). The recording electrode was driven down until contact was made with the cortex. This was recognized by an increase in the background noise level followed, usually within 100–200 μm, by a cell death. Thence forward, the electrode was advanced at 1 μm steps using an electrically driven Kopf microdrive. Conventional differential amplification and filtering (band pass: 60–6,000 Hz) were used to record the activity of single units isolated by the electrode. Extracellularly recorded action potentials were monitored both aurally on an audio amplifier and visually on a cathode ray oscilloscope.

The stereotaxic head holder used in these experiments was similar to that described by Bishop, Kozak, Levick & Vakkur (1962). The animal's head, but not its body, was tilted forward 12·5° to the horizontal so as to bring the visual axis parallel to the floor and perpendicular to the tangent screen. The general arrangement of the cat and the hand-plotting table has previously been described (Bishop *et al.* 1971). All receptive fields were plotted using hand-held visual stimuli. Slits or spots of light were projected on the plotting table by means of a hand-held Keeler Projectoscope and black targets were made from thin cardboard. The minimum response receptive fields (Barlow, Blakemore & Pettigrew, 1967) were plotted on sheets of paper and kept as a permanent record of the location and general properties of each isolated unit.

Stimulating electrodes were constructed from platinum-iridium wire (0·008 in. in diameter; 80% platinum, 20% iridium) insulated with glass. The exposed tip commonly protruded about 1 mm from the end of the insulation. Electrical pulses (50–200 μsec) of 0–100 V were generated by Tektronix pulse and wave-form generators. The stimulating electrodes were isolated using an Ortec Isolator. The bipolar stimulating configuration was always used. Photographic records of electrical stimulation were obtained using a Grass camera and latencies were checked by projecting the film through a Leitz 1 C enlarger and comparing the measured distances with calibration pulses previously photographed from the oscilloscope. The criteria for recognizing orthodromic and antidromic activation were similar to those described by Bishop, Burke & Davis (1962) and are described more fully elsewhere (Harvey, 1980).

The data are taken from experiments performed on twenty-four adult cats. In eighteen of these animals, a pair of stimulating electrodes was placed in the optic chiasm (HC; anterior 15–16 mm, lateral 1·5 mm) and optic radiation (HC; anterior 6 mm, lateral 8 and 10 mm). Field potentials recorded in area 18 were used to check that the electrodes were at the optimal depth. Generally, the recording electrode entered the cortex between HC; posterior 1 and 5 mm. All penetrations in area 18 passed down the lateral bank of the lateral gyrus and crossed the 17–18 border zone. To extend the traverse of area 18, the electrode was tilted with its tip angled laterally by about 10°. The cytoarchitectonic criteria used to define the 17–18 border and the correlation between the histological and physiological estimates of the border zone are discussed in the following paper (Harvey, 1980). Electrolytic lesions (5 μA/5–7 sec, tip negative) were made at various points during the recording penetration (Pl. 2). After the experiment, the animal was deeply anaesthetized with intravenously administered Nembutal and perfused through the heart with 10% formal saline. Nissl-stained frozen sections (40 μm thickness) were then prepared to reconstruct the electrode tracks. Shrinkage of the cortical tissue was estimated by measuring the distance between lesions and comparing this with the distance obtained from the Kopf microdrive while the recording was in progress. The positions of the stimulating electrodes were also checked either by gross dissection or histologically by sections prepared in a way similar to that used for identifying the locations of the recording electrodes. Only those units which were unambiguously located in area 18 have been included in the present analysis.

In one cat, [^{3}H]proline was injected under pressure through a micropipette into the main laminae of the d.l.g.n. The injection delivered 1 μl. (10 μc) of [^{3}H]proline. After 24 hr, the animal was anaesthetized with Nembutal and perfused through the heart with neutral buffered paraformaldehyde. The blocks of brain were fixed for several hours and then placed in a 30% sucrose solution in a 0·1 M-phosphate buffer until they sank. Frozen sections 40 μm thick were dipped in Nuclear Track emulsion NTB2 (Kodak), exposed to the radiation for 5 weeks and then developed in D19 developer (Kodak) and fixed with Kodak rapid fixer. The sections were lightly counterstained with cresyl violet.

RESULTS

Scheme of lamination in area 18

An unambiguous definition of the laminar pattern in area 18 is necessary for the interpretation of the present results. An example of a Nissl-stained section of area 18 is shown in Pl. 1*A*, and the criteria for recognizing the various laminae are described below.

Lamina I. As in area 17, lamina I in area 18 is a predominantly cell-free zone which lies immediately beneath the pial surface.

Lamina II–IIIa. Both Otsuka & Hassler (1962) and Garey (1971) have described layer II as being predominantly composed of small pyramidal cells and these cells can be clearly seen in Pl. 1*A*. However, due to the difficulty in determining where lamina II ends and lamina IIIa begins, this superficial region is here termed lamina II–IIIa.

Lamina III. The broadness of lamina III is perhaps the most significant cytoarchitectonic feature of the parastriate cortex and the lower aspect of this layer is situated about half-way through the thickness of the cortex. Otsuka & Hassler (1962) subdivided this lamina into two parts: IIIa and IIIb. IIIa is composed of small to medium pyramids, while IIIb contains a mixture of large, medium and small cells. The increase in the size of pyramidal neurones is evident in Pl. 1*A*, and this lamina has also been subdivided (IIIa and IIIb) in the present study. Due regard was given to the differences in cell size, but because of the difficulty in determining exactly where the large lamina III pyramids begin, layer III has been divided in half and laminae IIIa and IIIb are regarded as being of equal thickness.

Lamina IV. After an injection of [^{3}H]proline into the d.l.g.n., terminal labelling in area 18 is mostly confined to a band which lies between the large pyramidal cell bodies of lamina III and lamina V (Pl. 1*B*). Within this band, two sublaminae are evident. Immediately below the large pyramidal cells at the base of lamina III, there is a layer composed of loosely packed, medium-sized cells. This has been called lamina IVa. Beneath this layer is a band of small, densely packed cells which has an appearance similar to the granular layer of area 17. This has been designated lamina IVb (Pl. 1*A*, *B*).

Lamina V. This is a sparsely filled layer containing a number of large pyramidal cells. The equivalent of lamina Va of area 17 has not been recognized in the parastriate cortex.

Lamina VI. In contrast to lamina V, lamina VI is a more densely packed region which contains mostly medium-sized pyramidal cells. An input to lamina VI from the d.l.g.n. was not readily apparent (Pl. 1*B*) although both Rosenquist *et al.* (1974) and LeVay & Gilbert (1976) have reported that a weak but significant projection does occur.

Receptive field properties of area 18 neurones

Receptive field classification

The terminology of Henry (1977), originally designed for area 17, has proved equally useful in the classification of area 18 cells and the general properties of the various parastriate receptive field types are outlined below.

S and A cells. S cells can be divided into spatially separate light and/or dark edge response regions when tested with light and dark edges moved across the receptive field (cf. Bishop & Henry, 1972). Of the 117 S cells for which edge regions were plotted, forty (34 %) responded to only one edge (twenty-seven to dark and thirteen to light edge), sixty-nine (59 %) responded to both light and dark edges, and eight (7 %) had more than two edge response regions. Using moving stimuli, the mean separation of the primary borders (the primary borders run parallel to the optimal orientation) of individual light or dark edge response fields in S cells was found to be 0·93°. Cells which are excited by only one contrast of edge resemble other S cells in their general visual properties (see below) and the observation that they only respond to one edge when tested with hand-held visual stimuli is not felt to be a sufficient justification for putting them in a separate class. Cells of this kind have thus been placed in the S category. Indeed, there is evidence (R. Camarda, in preparation) that quantitative analysis of receptive fields sometimes reveals a second response region that is too weak to recognize using qualitative methods. Forty-three S cells (37 %) responded to stimulus movement in only one direction and thus were completely direction-selective. Sixteen S cells (14 %) showed no direction selectivity whatsoever, responding equally well to an optimally oriented stimulus moved in either direction. The remaining S cells showed various degrees of direction selectivity. It is worth noting here that although area 18 cells typically respond optimally to stimulus speeds of about 10–25°/sec, many cells (especially S cells located near the area centralis) will respond to slower velocities (1–2°/sec).

When tested with stationary flashing stimuli, S cells can usually be subdivided into spatially separate ON and/or OFF areas. Narrow bars of light flashed on and off in the receptive field often evoked only weak responses in parastriate S cells. In

these circumstances, it was difficult to find areas which gave pure ON or pure OFF responses. However, the receptive fields of parastriate S cells are generally larger than those of area 17 and it became evident that wider bars were often necessary to elicit strong, consistent responses. It is possible that this observation results from the fact that the larger subunits which make up area 18 S cell receptive fields may require substantial summation across the width of the flashing bar before an optimal response is obtained. Using these broad stimuli, almost all S cells could readily be subdivided into separate ON and/or OFF areas.

Of the 105 S cells tested with stationary flashing stimuli, thirty-nine (37%) possessed only one stationary flashing light field (thirteen units responded only to ON and twenty-six responded only to OFF), fifty S cells (48%) had spatially separate ON and OFF regions and a further three units had three ON and OFF areas. Tretter *et al.* (1975) have put cells which possess only one stationary flashing light receptive field into a separate group from cells in which both ON and OFF areas can be recognized. In the present study, cells with one or more ON or OFF regions have all been classed as S, primarily because quantitative analysis often reveals a second discharge area in cells thought to possess only one ON or OFF region when tested with hand-held stimuli (R. Camarda, in preparation). Thirteen cells did not respond to stationary stimuli; however their responses to moving stimuli were similar to other S cells and they have thus been placed in this category. Additional characteristics of area 18 S cells are that they usually have no or only low spontaneous activity and they are generally sharply tuned for stimulus orientation. The range of orientations over which cells continued to respond was measured for 115 S cells. Some S cells ceased to respond when the stimulus was oriented as little as 11° from the optimal while others continued to respond to stimuli angled 60° from the preferred orientation. On average, parastriate S cells will not respond to stimuli angled more than 30 to 35° from the optimal orientation.

Not all cells with spatially separate dark and light edge response fields have been classed as S. Very rarely (three out of 223 visually classified units), a cell was encountered which exhibited these properties but whose edge response regions were quite unlike those of S cells. These cells have large receptive fields (primary border separation of about 3·5°) and their response to a moving edge is sustained across the whole width of the receptive field. Their responses are more typical of C cells than S cells, since S cells always possess a region of maximum discharge within the receptive field. The large field cells just described are similar to the complex cell with non-uniform receptive field originally described by Hubel & Wiesel (1962) and have been designated as A cells (Henry, 1977).

C and B cells. A substantial number of parastriate neurones have spatially coincident light and dark edge response regions. In addition, they give mixed ON and OFF discharges over the entire receptive field when tested with stationary flashing stimuli. Cells with these properties have been divided into two basic categories and are termed C and B. C cells generally have large receptive fields (the mean separation of the primary borders was 4·7°) and have a relatively high rate of spontaneous activity (between 5 and 20 spikes/sec). They are broadly tuned for stimulus orientation and on average will continue to respond to stimuli inclined up to 50° from the preferred orientation. The response of C cells to a moving stimulus does not peak at

any particular location but is maintained across the width of the receptive field. In C cells, summation along the length of the stimulus varies from cell to cell. Of the fifty-nine C cells encountered in the present study, fourteen (24 %) resembled the striate cells described by Palmer & Rosenquist (1974) in that small spots of light moved in the preferred direction anywhere within the receptive field were as effective in driving the cell as an elongated stimulus. In the remaining C cells, lengthening the stimulus increased the response; in twelve cells, no response was obtained with small stimuli and very long edges (up to 10°) were required for consistent activation. Twenty-four C cells (42 %) responded to only one direction of movement and nine (16 %) were driven equally well by movement in either direction. C cells which responded to spots of light were more direction-selective than cells which responded best to elongated stimuli (cf. Harvey, 1980). Units designated as B cells (cf. Henry *et al.* 1978) are similar to C cells in that their light and dark edge regions are superimposed and stationary stimuli elicit mixed ON and OFF discharges. However, they resemble S cells in that they have smaller receptive fields (mean primary border separation of 1·6°), have low spontaneous activity and are sharply tuned for stimulus orientation. B cells cease to respond when stimuli are angled more than 30° from the preferred orientation.

The H or hypercomplex property. Some parastriate S, C and B cells responded optimally to stimuli of restricted length, indicative of the presence of inhibitory areas beyond the lateral borders (the lateral borders run perpendicular to the optimal orientation) of the receptive field. End-zone inhibition is the characteristic feature of hypercomplex cells (Hubel & Wiesel, 1965) and units exhibiting this property have been designated S_H, C_H and B_H (Henry, 1977). In the present study, hypercomplex properties were attributed to cells in which it was possible, by ear, to detect a decrease in the response as the stimulus was extended beyond an optimal length (cf. Rose, 1977; Kato, Bishop & Orban, 1978).

Non-oriented units. Forty-six units, recorded in the grey matter of area 18, were monocular and had concentrically organized receptive fields typical of thalamocortical afferent fibres (the term 'thalamocortical' is used rather than 'geniculocortical' because area 18 receives a substantial projection from the m.i.n. as well as from the d.l.g.n.). The central regions of these non-oriented units were mapped by flashing small spots of light at different locations within the receptive field. Centre diameters ranged from 0·7° to 2·7° and of the thirty-nine afferent fibres for which receptive fields were plotted, twenty had ON and nineteen had OFF centres. The responses to flashing stimuli were typically transient and the fibres usually responded best to fast stimulus movements. After repeated OR stimulation, these fibres showed no latency variation and continued to respond at frequencies of up to 1,000 Hz, indicative of direct activation of the axon (cf. Fig. 6). Rarely, non-oriented units were encountered which were activated trans-synaptically after OR stimulation. A similar small number of non-oriented cortical cells has also been found in area 17 (Henry, Harvey & Lund, 1979).

The relative encounter frequencies of area 18 cell classes

Of the 366 units isolated in area 18, 223 were unambiguously classed according to the criteria described above. Some of the remaining units were tested with electrical

stimulation but were lost before the unit could be visually classified, while in other units visual responses were too weak and inconsistent for classification to be made with confidence. S cells were the most commonly encountered cell type, making up 53% of the population of visually classed cells. C cells comprise 26% and B cells 4% of this population while S_H and C_H cells each contribute about 6% to the total. Parastriate cells with response properties characteristic of S or simple cells have also been described by Tretter *et al.* (1975), Dreher & Cottee (1975), Orban & Callens (1977), Yamane, Nikara & Sugie (1977) and Hammond & Andrews (1978). Most of these studies agree that S cells make up somewhere between 40–60% of the parastriate cell population.

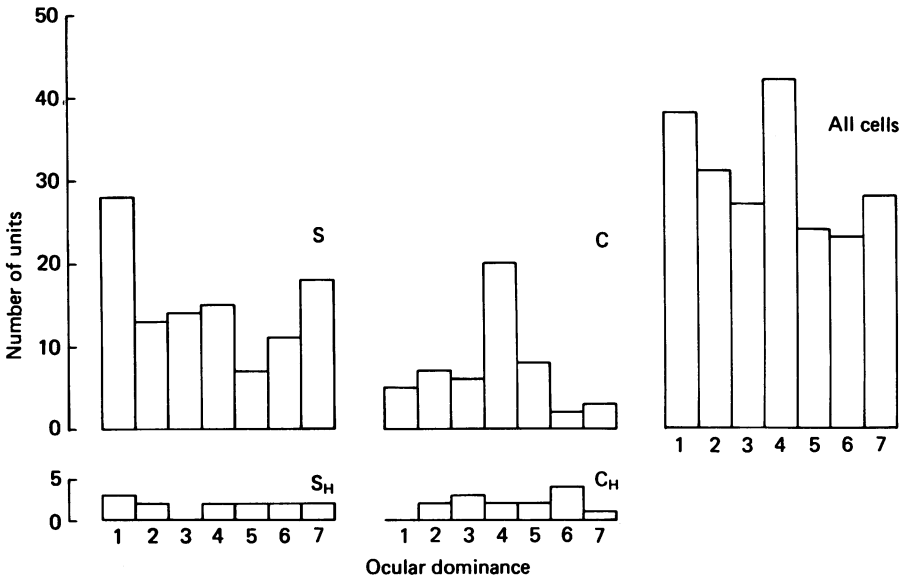

Fig. 1. Ocular dominance distributions of the four most common types of parastriate neurone and the over-all distribution for all cells in area 18. Ocular dominance expressed on a scale ranging from 1 (driven solely from contralateral eye) to 7 (driven solely from ipsilateral eye) (cf. Hubel & Wiesel, 1962).

Binocularity of cell types

Fig. 1 shows the degree of binocularity (see legend) of the four most common types of parastriate neurones, as well as the ocular dominance distribution for all cells in area 18. It should be noted that it was not possible to make an estimate of the ocular dominance in all cells. Further, some cells which could not be satisfactorily placed in one of the receptive field classes were, nevertheless, classified with regard to their ocular dominance. It is clear that more cells in the S family (both S and S_H cells) are monocularly activated than cells in the C family (C and C_H cells); 44% of S type cells were driven by only one eye compared to 16% of cells in the C family.

Receptive field classes and visual field eccentricity

All electrode penetrations passed down the lateral bank of the lateral gyrus (Pl. 2) and so crossed the 17–18 border zone. Units in area 18 recorded close to this border region have centrally located receptive fields, and these fields move out in a horizontal direction as the electrode moves deeper down the lateral bank (cf. Fig. 1 in Harvey, 1980). The location of receptive fields with respect to elevation in the visual field is related to the anterior–posterior position of the electrode penetration; most units in the present study had receptive fields in the inferior visual field, no further than 5 or 6° below the area centralis. The visual field eccentricity of cells for which receptive fields were plotted was determined by measuring the distance between the receptive centre and the ophthalmoscopically estimated position of the area centralis; for binocularly driven units, the mean eccentricity for the two eyes has been used. One hundred and four cells had receptive fields located within 4° of the area centralis and 122 had more peripheral fields. Cells with receptive fields within 4° of the area centralis and cells with receptive fields at eccentricities greater than 4° have been termed central and paracentral respectively (cf. Albus, 1975).

The relative encounter rates of central and paracentral S and C cells are remarkably similar; S cells made up 51·9 % and 51·6 % of all cells located in central and paracentral visual fields, while C cells comprised 22 % and 27 % of the total populations found in the two visual regions. From the histological reconstruction of electrode paths there was no tendency to record more frequently from a given lamina in regions of cortex devoted to central rather than paracentral visual processing. Thus the encounter rates described above are not biased by differential sampling of different regions of central and paracentral cortex, and it would seem that S and C cells are distributed evenly throughout the visual representation in area 18 (at least up to eccentricities of 20°). There is a tendency for monocular cells in area 18 to occur more often in the central visual field; 38 % of centrally located cells were monocular compared with 25 % of paracentral cells. This result is similar to that reported by Albus (1975) in area 17, although the effect of eccentricity appears to be less pronounced in area 18. Considering the S family, 51 % and 35 % of cells were monocular in the central and paracentral visual fields respectively. In comparison, the proportions of monocular cells in the C family were 18 % centrally and 11 % paracentrally. Receptive fields in area 18 increase in size as one moves from central to peripheral visual areas (cf. Hubel & Wiesel, 1965; Dreher & Cottee, 1975). When plotted with moving stimuli, the average separation of the primary borders of central C cells was 3·5°, compared with 5·6° for cells located in the paracentral visual field. The effect of increasing eccentricity on receptive field size was less marked in S cells; the mean primary border separation for individual light or dark edge response regions was 0·87° and 0·96° in central and paracentral visual areas respectively.

Laminar distribution of receptive field classes

The laminar position of physiologically identified units was obtained from the histological reconstruction of electrode tracks. Such a penetration and its reconstruction are shown in Pl. 2 and Fig. 2. Due to the errors inherent in such reconstructions (Henry *et al.* 1979), units found to be located at the borders between laminae

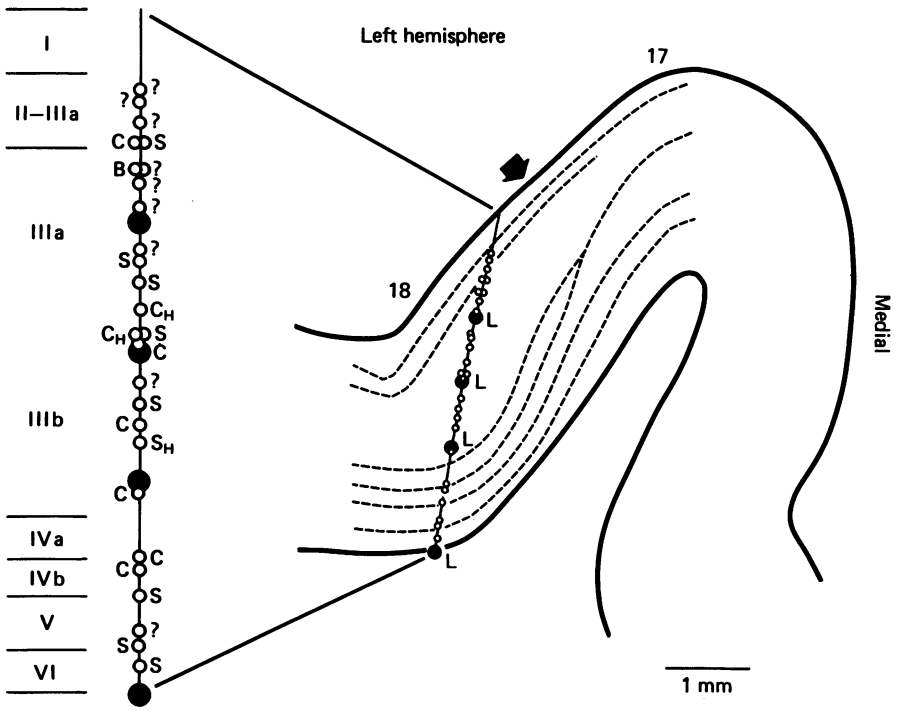

Fig. 2. Histological reconstruction of the electrode track presented in Pl. 2, showing the location of single units recorded during the penetration. Receptive field types and laminar boundaries are defined in text. L, electrolytic lesions; arrow, 17–18 border region; ?, unclassified units.

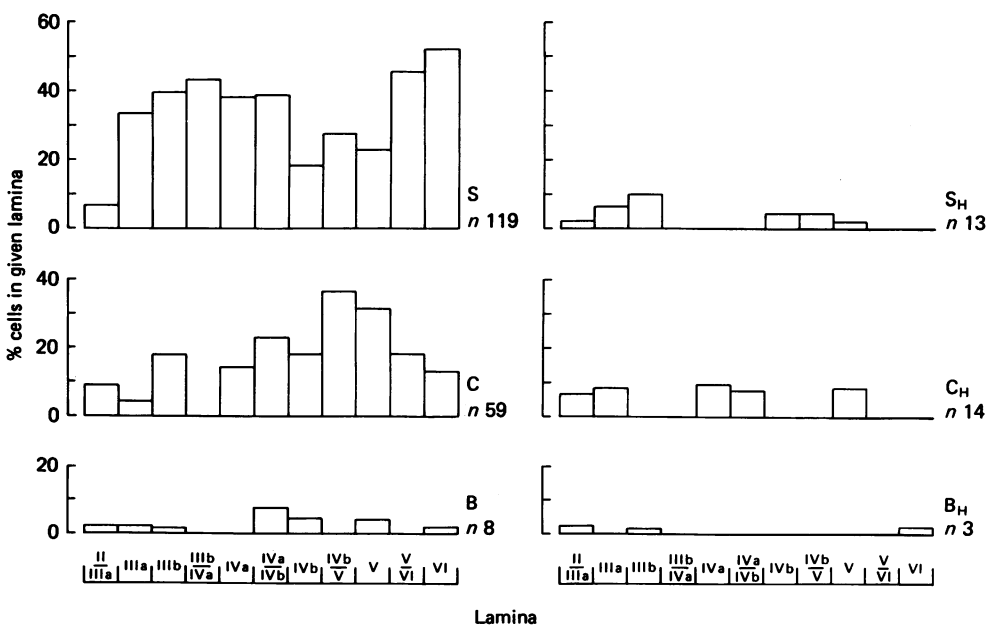

Fig. 3. Laminar distribution of the major cell classes in area 18. For each cell type the proportions in each lamina are expressed as a percentage of the total number of cells encountered in that lamina. *n*, total number of cells in each class.

have not been assigned to any particular layer, but have been placed in separate border groups. In the present study, laminar analysis has been made easier by the fact that most of the electrode tracks ran parallel to the laminar boundaries.

The laminar distribution of the major cell types in area 18 is shown in Fig. 3. In this Figure, the proportions of the major cell types in each cortical lamina are expressed as a percentage of the total number of cells isolated in each layer. Such an analysis removes the effects of uneven sampling in different laminae. The proportion of S cells is highest in laminae IIIb, IVa and VI, and their distribution is therefore very similar to the laminar pattern of geniculocortical fibre termination. Unlike area 17 (Henry *et al.* 1979), there is no indication that the ocular dominance of S cells varies from layer to layer. C cells are commonly found in laminae IVb and V; C cells which responded well to spots of light are not distributed any differently from the rest of the C population. Cells with hypercomplex properties are often located in the superficial layers (54 % of all end-stopped cells are found in layers II and III), as are cells which were apparently unresponsive to visual stimulation. In general, the laminar distribution of receptive field classes in area 18 is strikingly similar to that found in area 17 (cf. Henry *et al.* 1979). Finally, thalamocortical fibres were recorded throughout the middle to deep layers of area 18 but were never encountered above lamina IIIb.

The thalamic input to area 18

Electrical stimulation of the OR and OX was tested on 282 cells and twenty-nine thalamocortical afferents. Of the cell population, 200 (71 %) could be orthodromically driven from one or both stimulating sites; 151 were excited from both OR and OX, forty-three were excited from only OR and six were driven from only OX.

Units responding to only OR stimulation

Forty-three cells in area 18 were activated by OR stimulation but could not be driven from the optic chiasm. The OR latencies ranged from 1·0 to 8·5 msec. Twenty-four of these neurones had latencies greater than 2·0 msec and were therefore not directly excited by fast thalamocortical fibres (see below). The nature of the afferent input to these cells will be further considered in the Discussion.

Units responding to both OX and OR stimulation

One hundred and fifty-one cells were orthodromically activated from both OX and OR stimulating electrodes. The *minimum* latencies to OX and OR stimulation are shown in the two histograms of Fig. 4. There appear to be two main peaks in both the OX and OR latency distributions (as indicated by the small arrows). The bimodality of the latency distribution is also evident in Fig. 5, which presents the minimum latencies to both OX and OR stimulation for each cell (filled circles). Before analysing this data further, however, it is instructive to examine the OX and OR latencies of thalamocortical fibres recorded in the grey matter of area 18.

OX and OR latencies of thalamocortical fibres. The open circles in Fig. 5 show the OX and OR latencies for twenty-seven thalamocortical axons excited from both stimulating sites. An example of an afferent fibre excited by OX and OR stimulation is shown in Fig. 6; the minimum latencies to OX and OR stimulation were 1·4 and

0·42 msec respectively. Note that after OR stimulation the fibre shows no latency variation. The mean OX and OR latencies for thalamic afferents recorded in area 18 are 1·55 msec and 0·5 msec respectively, giving a mean OX – OR latency difference of 1·05 msec. This difference is shown as the line in Fig. 5; the line is drawn through all points at which the OX latency is equal to the OR latency plus 1·05 msec. Since there is one synapse interposed between the OX and OR stimulating electrodes, an OX – OR difference of 1·05 msec indicates that the fibres involved in the retino-

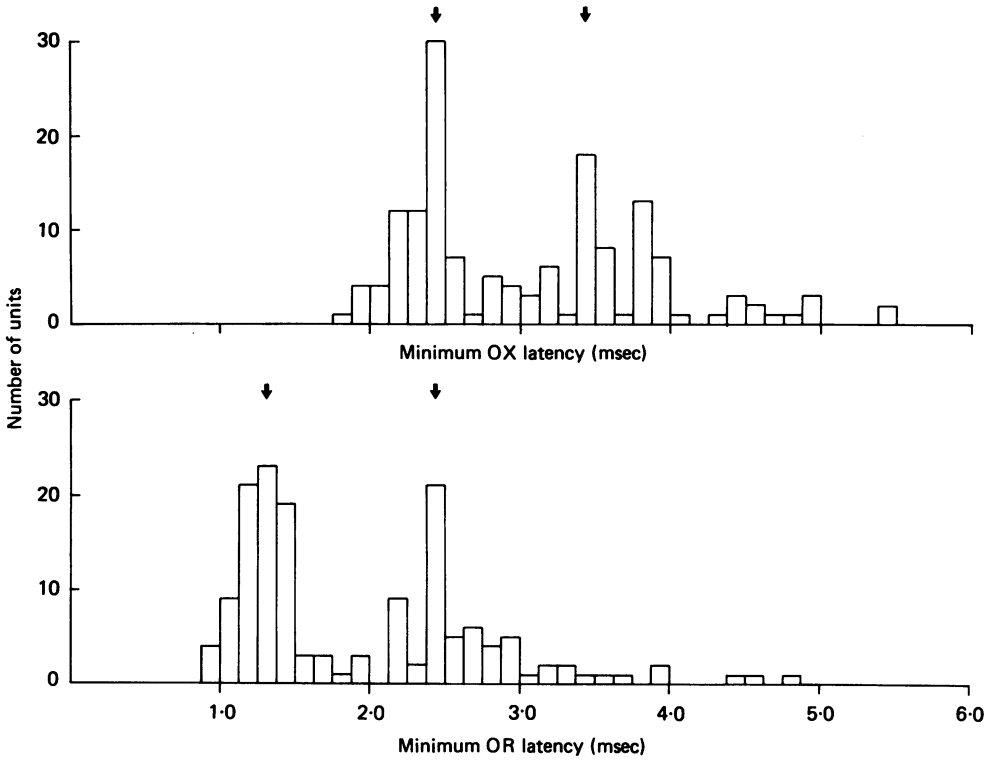

Fig. 4. Minimum orthodromic latencies of parastriate neurones excited after optic chiasm (OX) and optic radiation (OR) stimulation. Arrows indicate peaks in the latency distributions.

thalamo-parastriate pathway are fast conducting. The short OR latencies of fibres entering area 18 (cf. Fig. 5) support this proposition. The observation that short OR latencies are correlated with small OX – OR differences suggests that fast retino-thalamic fibres synapse on cells giving rise to rapidly conducting thalamocortical axons (cf. Cleland, Dubin & Levick, 1971; Hoffmann, Stone & Sherman, 1972; Cleland, Levick, Morstyn & Wagner, 1976).

OX and OR latencies of cortical cells. As shown in Fig. 5, cortical cells excited from both OX and OR have been divided into two latency groups, group 1 and group 2. Cells with OX latencies between 2·0 and 3·0 msec, and OR latencies between 1·0 and 2·0 msec, have been placed in the group 1 category. Two cells with OX latencies less than 2·0 msec have also been included in this group. Group 2 neurones are defined

as having OX latencies between 3·0 and 4·0 msec and OR latencies between 2·0 and 3·0 msec. The limits of the groups are admittedly somewhat arbitrary, however later analysis will provide strong justification for the subdivision. The remaining cells which have OX and OR latencies which do not fall within either of the above groups have been put into a third group. An example of a group 1 neurone excited from OX and OR is presented in Fig. 6. The minimum OX and OR latencies of this cell were 2·4 msec and 1·25 msec, respectively. The latency variation is characteristic of trans-synaptic responses.

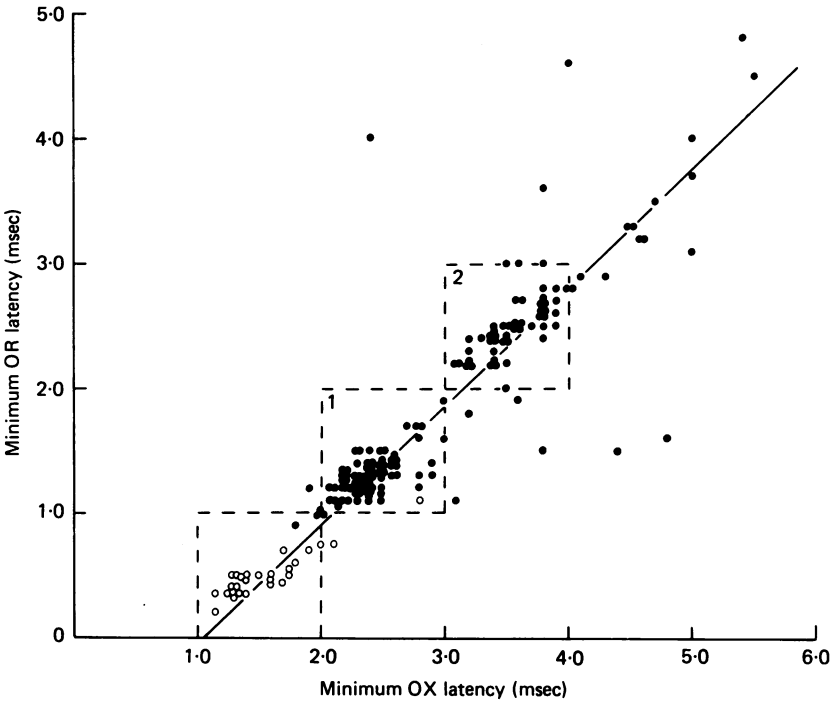

Fig. 5. Orthodromic optic chiasm (OX) and optic radiation (OR) latencies of parastriate neurones (filled circles) and thalamocortical fibres (open circles) recorded within the grey matter of area 18. The line represents the mean OX − OR latency difference (1·05 msec) of thalamocortical fibres and passes through all points at which the OX latency is equal to the OR latency plus 1·05 msec. For further explanation, see text.

The mean OX and OR latencies for group 1 neurones (n = 78) are 2·4 and 1·3 msec respectively, and the mean latencies to OX and OR stimulation for group 2 neurones (n = 52) are 3·6 and 2·5 msec. The OR − OX latency difference for both groups is therefore 1·1 msec; thus although the *absolute* OX and OR latencies of group 2 neurones are a millisecond or so longer than those of group 1 cells, this increase does not appear to be related to the speed of conduction of the afferent axons. Since the mean OX − OR difference for thalamocortical fibres is almost identical to the mean OX − OR differences for both group 1 and group 2 neurones, it can be concluded that the axons recorded presynaptically in area 18 belong to the same population as those innervating parastriate neurones. This being so, it is significant that nearly

all group 1 *and* group 2 cells lie close to the line which represents the mean OX – OR difference for thalamocortical fibres (Fig. 5). This result provides further indication that the difference in latencies between group 1 and group 2 neurones is not due to variation in the conduction velocity of afferent fibres. The longer group 2 latencies must therefore arise from delays within the cortex itself.

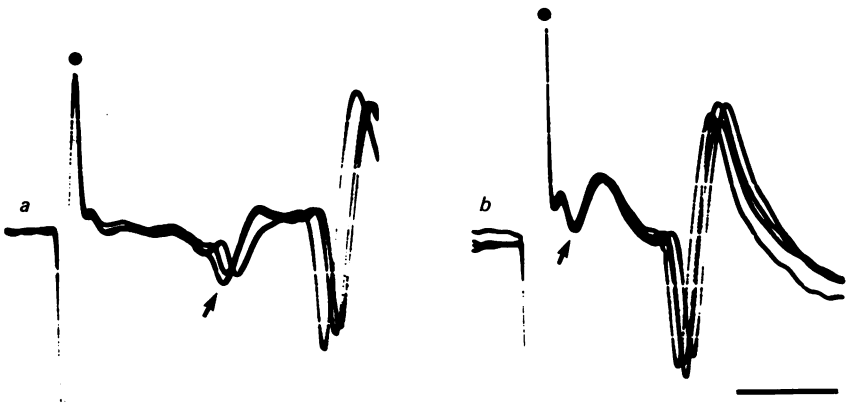

Fig. 6. Orthodromic activation of a thalamocortical fibre (arrowed) and a group 1 neurone recorded in area 18. *a*, optic chiasm stimulation; *b*, optic radiation stimulation. Time marker, 1 msec.

The average OR latency difference between afferent fibres and group 1 neurones is 0·8 msec and between group 1 and group 2 neurones is 1·2 msec. The latency difference (0·8 msec) between the afferent axons and the post-synaptic group 1 cells is presumably a measure, for the most part, of the synaptic transmission delay but may also include some conduction time within the terminal field of the afferent fibre. The longest OR latency for a thalamocortical fibre was 1·1 msec, hence cells with orthodromic latencies greater than 1·9 msec are unlikely to be monosynaptically excited. Similarly, the fastest afferent fibre response to OR stimulation was 0·3 msec, thus assuming a transmission delay of about 0·8 msec, the earliest possible disynaptic response is again 1·9 msec. These arguments provide justification for the subdivision between group 1 and group 2 proposed above and strongly suggest that group 1 and group 2 cells are monosynaptically and disynaptically excited respectively. The average OR latency difference between groups 1 and 2 is 1·2 msec. The additional delay of 0·4 msec over and above the 0·8 msec described previously is probably related to the extra conduction time taken for the nerve impulse to travel within the cortex from the group 1 to the group 2 cell.

Laminar distribution of cell groups defined by afferent stimulation

In Fig. 7 the relative proportions of group 1 and group 2 units and cells that could not be driven by electrical stimulation are shown for each cortical lamina. The proportions of each group are shown as percentages; they are derived by dividing the number of cells in each group in a particular lamina by the total number of cells tested by electrical stimulation in that lamina. The stippled bars indicate the anatomically defined termination of geniculocortical fibres in area 18. Group 1 cells

are found most often in laminae IIIb, IVa, IVb and VI; up to about 50% of all neurones encountered in layers IIIb and IVa were classed as group 1 cells. Note the sharp decrease in the proportion of group 1 cells in lamina V. In general, the distribution of group 1 neurones closely follows the anatomically defined laminar distribution of afferent terminals (Pl. 1*B*) and is consistent with the suggestion that group 1 neurones are directly activated by thalamocortical fibres. Group 2 neurones

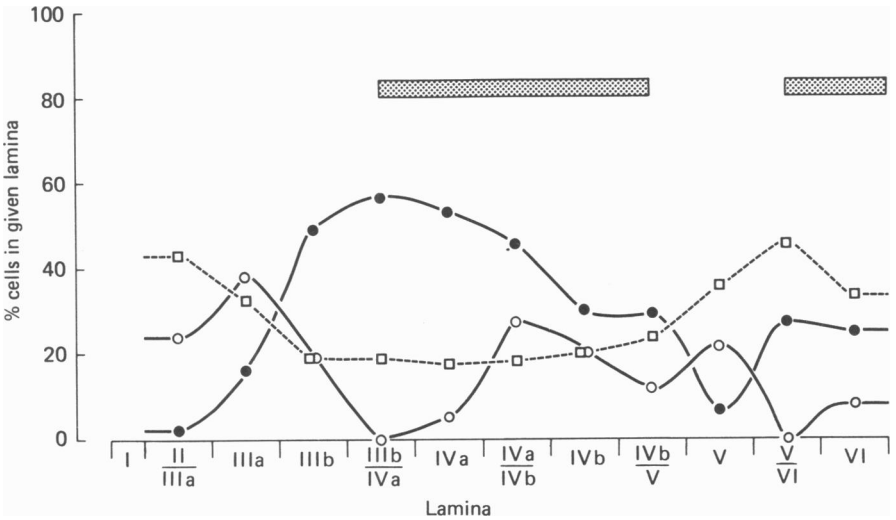

Fig. 7. The relative proportions, in each parastriate cortical lamina, of group 1 and group 2 cells and cells not excited by electrical stimulation. Stippled bars, anatomically defined termination of geniculocortical fibres. ●, Group 1; ○, group 2; □, not driven.

predominante in layers II–IIIa, IIIa and V (shown anatomically to receive very few thalamic axons) and are very rare in laminae IIIb and IVa. These observations lend support to the suggestion that group 2 neurones are indirectly activated from the optic radiation. Units not excited by either OX or OR stimulation are chiefly located in laminae II–IIIa, IIIa, V and VI. A number of cells in group 3 have OX and OR latencies of more than 4·0 and 3·0 msec respectively, yet have OX − OR latency differences indicative of innervation by fast conducting afferents (Fig. 5). If these presumably indirectly excited cells are considered along with group 2 neurones, then over 30% of all units encountered at the IVb–V border and in layer V itself appear to be indirectly driven from the optic radiation. Cells driven only from OR (not shown in Fig. 7) are found most often in laminae II–IIIa and VI.

Receptive field properties of cell groups defined by afferent stimulation

The receptive field properties of the 282 cells for which OX and OR stimulation was attempted are shown in Table 1. The majority (53%) of S cells are group 1 neurones, while only 10% of all S cells have latencies suggestive of an indirect input from the thalamus; in all, 84% of parastriate S cells were excited from at least one stimulating site. For S cells activated from both OX and OR, 81% of S cells with only one edge response area are group 1 cells, compared with 76% of S cells with two or more edge regions. Thus cells with one or more edge response regions are very

similar in their afferent connectivity and this gives further support to the proposition that they should all be placed in the S category. There is no indication that group 2 S cells have larger receptive fields than group 1 S cells.

Only 18% of C cells have OX and OR latencies indicative of a direct thalamo-cortical input; most C cells (49%) are group 2 neurones. Many of the C cells in group 3 have OX and OR latencies greater than 4·0 and 3·0 msec respectively (see above), and if these particular cells are considered along with group 2 neurones, then about

TABLE 1. The afferent connectivity of parastriate receptive field classes

	Latency group						
	1	2	3	OR only	OX only	N.e.s.	Total
S	43	8	3	10	4	13	81
S_H	7	2	0	0	0	2	11
C	7	19	8	3	0	2	39
C_H	1	7	2	1	0	1	12
B	1	3	2	0	0	0	6
B_H	0	1	0	1	0	1	3
A	1	0	0	0	0	0	1
N.o.	2	0	0	0	0	1	3
N.v.c.	16	12	6	28	2	62	126

N.e.s., not driven by electrical stimulation;
N.v.c., not visually classified;
N.o., non-oriented.

60% of all C cells have OX and OR latencies suggestive of indirect activation from the optic radiation. In all, 95% of parastriate C cells were activated after OX and/or OR stimulation. When compared with the over-all C population, C cells which show little or no length summation more often have group 2 latencies. As with S cells, the receptive fields of C cells in group 2 do not appear to be any larger than those in group 1.

S_H and C_H cells closely resemble their parent groups in terms of the proportion of each cell type with latencies suggestive of direct or indirect activation from the optic radiation (Table 1). Thus 64% of S_H cells are group 1 neurones whereas group 2 neurones comprise 59% of the C_H population. Note that six of the seven group 1 S_H cells were in lamina IIIb and all but one of the group 2 C_H cells were encountered in laminae II–IIIa and IIIa. Many of the cells which were not excited by electrical stimulation could not be readily classified using visual stimuli. It is possible that these apparently unresponsive neurones were damaged in some way by the proximity of the recording electrode. However, the absence of electrical and visual activation may also indicate that the excitatory input is mediated by a large number of intra-cortical synapses and that very specific visual stimuli are required to trigger these cells.

Multiple discharges evoked by electrical stimulation

Of the 194 cells responsive to OR stimulation, 137 (71%) gave only one impulse and fifty-seven (29%) gave two or more spikes for every OR shock. Fig. 8 shows the

latencies of the second and third spikes elicited after single shocks of the optic radiation. In twenty-six cells, second spikes were elicited after both OX and OR stimulation. The mean OX – OR latency difference for these spikes was 1·2 msec which is very similar to the 1·1 msec found for thalamocortical fibres and the first spikes of group 1 and group 2 neurones (cf. Fig. 5). Thus the longer OR latencies of second spikes (Fig. 8) seem not to be related to the speed of conduction of afferent

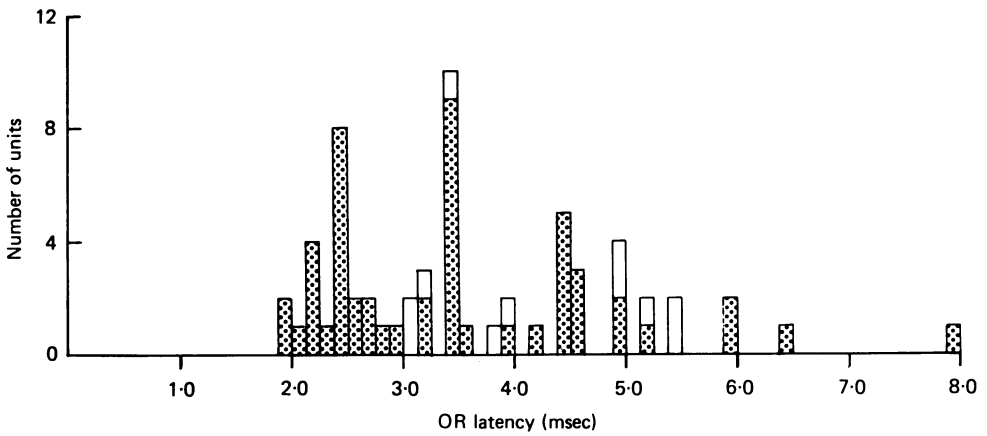

Fig. 8. Minimum orthodromic latencies of the second and third spikes elicited after single shocks of the optic radiation (OR). Stippled blocks, second spike latencies; open blocks, third spike latencies.

axons and may therefore result from extra delays within the cortex itself. In this regard, Tretter *et al.* (1975) have shown that in cells that fire repetitively after a single OR shock, each impulse is associated with its own discrete excitatory post-synaptic potential. It would appear, then, that the multiple discharges evoked by a single electrical shock may be mediated by polysynaptic pathways. The latencies of the second spikes peak at about 2·4 and 3·4 msec. Cells with second spike latencies around 2·4 msec were classed on the basis of their first spike OX – OR latencies as group 1 neurones and their second spike latencies are identical to the latencies of the *first* spike of group 2 neurones (mean OR latency = 2·4 msec). The coincidence of group 1 second spike and group 2 first spike latencies lends support to the suggestion that group 2 neurones are disynaptically activated by thalamocortical afferents. In agreement with Tretter *et al.* (1975), most S cells (83 %) gave only one spike per shock, whereas C cells (73 %) tended to give multiple discharges.

DISCUSSION

The thalamic input to area 18

In agreement with previous anatomical and physiological studies (see Introduction), nearly all of the afferent fibres recorded in the deeper layers of the parastriate cortex are fast conducting and have visual properties typical of Y type (Hoffmann *et al.* 1972) or brisk transient (Cleland *et al.* 1971) units. Furthermore, almost all

of the cells in area 18 excited from both the optic chiasm and optic radiation have latencies indicative of innervation by this same population of fibres.

Forty-three cells could be excited by OR but not by OX stimulation. Some of the OR latencies were long which could indicate either that long polysynaptic pathways are involved or that the afferent fibres mediating these orthodromic responses are slow conducting. Only one slowly conducting fibre was recorded presynaptically in area 18 but this may be due to the difficulty in recording from fibres which would presumably be of small diameter. The observation that many of the cells activated at long latency after OR stimulation occur in lamina II–IIIa is perhaps indicative of polysynaptic input; however the possibility that some slowly conducting axons project to area 18 cannot be ruled out. Some cells excited only from the OR had very short OR latencies. Lack of OX activation in general, but particularly in these cells, may either arise because the OR activation was mediated via the recurrent collaterals of efferent axons (cf. Harvey, 1980) or because the thalamocortical fibres originated from thalamic nuclei other than d.l.g.n. and m.i.n. In this context, a projection to area 18 has been described anatomically from the pulvinar region (Gilbert & Kelly, 1975; Maciewicz, 1975; Kennedy & Baleydier, 1977) and the lateral posterior nucleus (Niimi & Sprague, 1970; Hollander & Vanegas, 1977).

The processing of afferent information in area 18: a model

The electrophysiological data presented in this study has been incorporated into a tentative model (Fig. 9) which attempts to describe how afferent visual information passing through the d.l.g.n. and m.i.n. is processed within area 18. The evidence upon which this model is based can be summarized as follows. Group 1 cells are commonly found in laminae IIIb, IVa, IVb and VI. They are represented by the cells labelled 1 in Fig. 9 and are shown as receiving direct connexions from incoming thalamic fibres. Although pyramidal cells have been drawn, it should be stressed that some cells may have stellate morphology (Garey & Powell, 1971). Lamina VI neurones are shown as being directly excited in two possible ways: one via a thalamic terminal ending an on apical dendrite passing through layer IV, and the other by way of interaction between an afferent fibre and a basal dendrite in lamina VI. Many group 1 cells are found in layer IIIb, above the laminae in which geniculocortical terminals are concentrated (Pl. 1*B*). As shown in Fig. 9, it is proposed that these cells deep in lamina III have basal dendrites which reach down into layer IVa and perhaps IVb.

Group 2 neurones are commonly encountered in laminae II–IIIa, IIIa and V, and neurones in these layers are shown as receiving excitatory inputs from group 1 cells. Although the large pyramids in layer V have apical dendrites which pass up through layer IV, the fact that the majority of layer V neurones are indirectly activated from the thalamus suggests that these dendrites are not contacted to any significant degree by primary afferent terminals. Group 2 neurones often fire repetitively after a single optic radiation shock which suggests that there are multiple synaptic inputs onto these cells (cf. Tretter *et al.* 1975). One lamina III cell and one neurone in lamina V are shown as receiving an input from both a group 1 and a group 2 cell and hence are disynaptically and trisynaptically excited by thalamic afferents. Layer III, V and VI pyramidal cells are shown as having axons which project out

of the cortex. The afferent connexions of these corticofugal cells are described elsewhere (Harvey, 1980).

In terms of its afferent connectivity, layer IVb appears to be intermediate between laminae IIIb–IVa and lamina V. However, some of the units thought to be in lamina IVb may actually have their somata in, for example, layer V since one cannot be certain, using extracellular recording techniques, that the electrode is necessarily

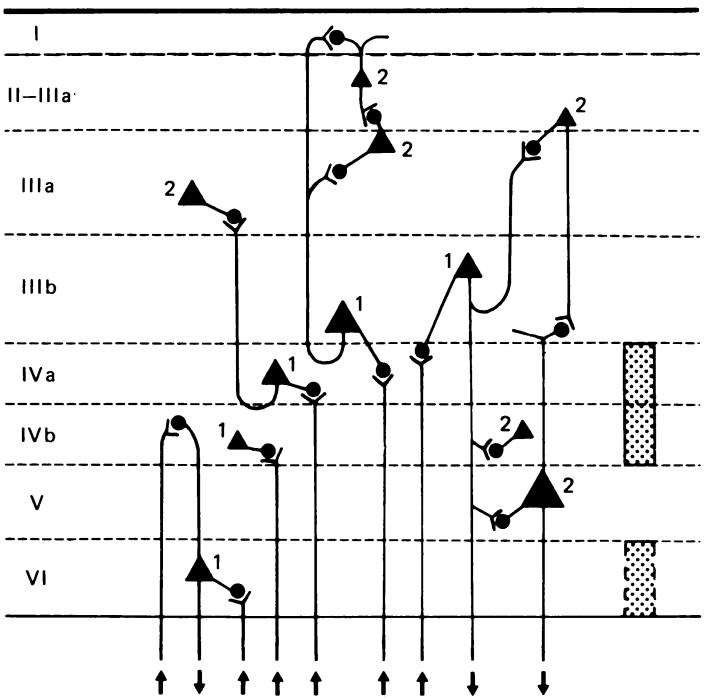

Fig. 9. A tentative model which depicts how incoming visual information is processed within area 18. The experimental basis for this model, as well as some of its implications are discussed in detail in the text. Cells labelled 1 and 2 represent group 1 and group 2 neurones respectively. Stippled bars on the right show the anatomically defined distribution of geniculocortical terminals.

positioned close to the cell body. Evidence that activity can be recorded at sites distant to the soma is presented in the following paper (Harvey, 1980), but it seems that this usually occurs only when the largest cortical cells are involved. The generally good correlation between the disposition of the electrophysiologically defined cell groups and the anatomical distribution of thalamic terminals supports this view. It should also be stressed that the scheme described above is only concerned with the excitatory pathways within the parastriate cortex since the technique of extracellular recording does not allow an analysis of inhibitory mechanisms. Intracellular studies may well reveal that parastriate group 1 and group 2 cells receive disynaptic and trisynaptic inhibition respectively as described by Toyama, Matsunami, Ohno and Tokashiki (1974).

Visual processing in area 18

The data presented in Table 1 indicate that the majority of S cells are directly excited while most C cells have OX and OR latencies suggestive of indirect activation by afferent fibres. Although it is not possible to identify the cells which are afferent to C cells, or which receive their input from S cells, the results are therefore to some extent consistent with the hierarchical model of Hubel & Wiesel (1962, 1965). However, a number of observations are inconsistent with this model. First, there are a few S cells with group 2 latencies and a small number of C cells which are monosynaptically excited by thalamic afferents. Interestingly, the group 2 S cells were all encountered in laminae which do not receive afferent fibres, while the group 1 C cells were always found between laminae IIIb and IVa. No discernible differences in the receptive field properties of group 1 and group 2 S cells or group 1 and group 2 C cells were found.

Secondly, Hubel & Wiesel (1965) proposed that hypercomplex or H cells were third order neurones. However, it is clear from the present work that many H cells (especially those classified as S_H neurones) are directly driven by afferent fibres. Indeed, the similarity in the afferent connexions of S_H and S, and C_H and C cells suggests that cells which possess the H property should not be regarded as a unique or separate cell type, but are a modification of already existing cell groups whose basic receptive field properties are predominantly determined by their afferent excitatory connexions. H cells in area 18 may only differ from their parent cell groups in as much as they receive a greater preponderance of intracortical inhibitory synaptic inputs. End-zone inhibition may also reflect, in part, the *absence* of afferent excitatory input resulting from inhibitory interactions at an earlier stage in the visual pathway such as that derived from the antagonistic effects of the surround and the suppressive field in d.l.g.n. neurones (Levick, Cleland & Dubin, 1972; Dreher & Sanderson, 1973).

It has been suggested that area 18 of the cat, because of its heavy Y input, is mainly concerned with processing information about the motion of objects in space, whereas area 17, which receives mostly X afferents, is primarily involved in high resolution tasks concerning the form and texture of visual stimuli (e.g., Tretter *et al.* 1975; Orban, 1977; Movshon, Thompson & Tolhurst, 1978). This separation of form and motion perception into separate parallel systems (i.e. areas 17 and 18) has psychophysical correlates (e.g. Tolhurst, 1973) and at first sight the concept is an attractive one. However, the present results indicate that the intrinsic organization of area 18 is very similar to area 17 (Henry *et al.* 1979), and from an examination of the receptive field properties of parastriate cells it would seem that area 18 is capable of discriminating both the elements of form and motion of objects in visual space. Perhaps, *within each area*, S cells are involved in the processing of form vision while C cells are primarily concerned with the temporal aspects of perception (cf. Creutzfeldt & Nothdurft, 1978). This concept receives support from the observation that cells in area 17 and area 18 efferent to the same subcortical site are more closely related than cells in the same cortical area projecting to different subcortical regions. Thus S and C cells in both the striate and parastriate cortex project to the d.l.g.n. and superior colliculus respectively (Harvey, 1980).

An alternative explanation might be that area 18 differs from area 17 in that it processes information derived from a different region of visual space. Levick (1977), for example, has suggested that the brisk transient system of the cat is primarily concerned with the analysis of stimuli close to the animal. Although it is not yet clear to what extent this hypothesis is applicable to the parastriate cortex itself, the relatively large receptive fields and responsiveness to fast stimulus movements characteristic of area 18 neurones makes them ideally suited for encoding information about objects of this kind.

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REFERENCES

ALBUS, K. (1975). Predominance of monocularly driven cells in the projection area of the central visual field in cat's striate cortex. *Brain Res.* **89**, 341–347.

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

BISHOP, P. O., BURKE, W. & DAVIS, R. (1962). Single-unit recording from antidromically activated optic radiation neurones. *J. Physiol.* **162**, 432–450.

BISHOP, P. O. & HENRY, G. H. (1972). Striate neurons: receptive field concepts. *Invest. Ophthal.* **11**, 346–354.

BISHOP, P. O., HENRY, G. H. & SMITH, C. J. (1971). Binocular interaction fields of single units in the cat striate cortex. *J. Physiol.* **216**, 39–68.

BISHOP, P. O., KOZAK, W., LEVICK, W. R. & VAKKUR, G. J. (1962). The determination of the projection of the visual field on to the lateral geniculate nucleus of the cat. *J. Physiol.* **163**, 503–539.

CLELAND, B. G., DUBIN, M. W. & LEVICK, W. R. (1971). Sustained and transient neurons in the cat's retina and lateral geniculate nucleus. *J. Physiol.* **217**, 473–496.

CLELAND, B. G., LEVICK, W. R., MORSTYN, R. & WAGNER, H. G. (1976). Lateral geniculate relay of slowly conducting retinal afferents to cat visual cortex. *J. Physiol.* **255**, 299–320.

CREUTZFELDT, O. D. & NOTHDURFT, H. C. (1978). Representation of complex visual stimuli in the brain. *Naturwissenschaften* **65**, 307–318.

DREHER, B. & COTTEE, L. J. (1975). Visual receptive-field properties of cells in area 18 of cat's cerebral cortex before and after acute lesions in area 17. *J. Neurophysiol.* **38**, 735–750.

DREHER, B. & SANDERSON, K. J. (1973). Receptive field analysis: responses to moving visual contours by single lateral geniculate neurones in the cat. *J. Physiol.* **234**, 95–118.

DREHER, B. & SEFTON, A. J. (1979). Properties of neurones in cat's dorsal lateral geniculate nucleus: a comparison between medial interlaminar and laminated parts of the nucleus. *J. comp. Neurol.* **183**, 47–64.

DUBIN, M. W. & CLELAND, B. G. (1977). Organization of visual inputs to interneurons of lateral geniculate nucleus of the cat. *J. Neurophysiol.* **40**, 410–427.

GAREY, L. J. (1971). A light and electron microscopic study of the visual cortex of the cat and monkey. *Proc. R. Soc. B* **179**, 21–40.

GAREY, L. J. & BLAKEMORE, C. (1977). Monocular deprivation: morphological effects on different classes of neurons in the lateral geniculate nucleus. *Science, N.Y.* **195**, 414–416.

GAREY, L. J. & POWELL, T. P. S. (1967). The projection of the lateral geniculate nucleus upon the cortex in the cat. *Proc. R. Soc.*, B **169**, 107–126.

GAREY, L. J. & POWELL, T. P. S. (1971). An experimental study of the termination of the lateral geniculate-cortical pathway in the cat and monkey. *Proc. R. Soc.* B **179**, 41–63.

GILBERT, C. D. & KELLY, J. P. (1975). The projections of cells in different layers of the cat's visual cortex. *J. comp. Neurol.* **163**, 81–106.

HAMMOND, P. & ANDREWS, D. P. (1978). Orientation tuning of cells in areas 17 and 18 of the cat's visual cortex. *Expl Brain Res.* **31**, 341–351.

HARVEY, A. R. (1977). A correlation of receptive field properties with afferent connections of cells in different laminae in areas 17 and 18 of the cat. *Proc. Aust. Physiol. Pharmacol. Soc.* **8**, 102*P*.

HARVEY, A. R. (1980). A physiological analysis of subcortical and commissural projections of areas 17 and 18 of the cat. *J. Physiol.* **302**, 507–534.

HARVEY, A. R. & CAMARDA, R. (1978). An examination of the hypercomplex property in the cat parastriate cortex. *Proc. Aust. Physiol. Pharmacol. Soc.* **9**, 191*P*.

HENRY, G. H. (1977). Receptive field classes of cells in the striate cortex of the cat. *Brain Res.* **133**, 1–28.

HENRY, G. H., HARVEY, A. R. & LUND, J. S. (1979). The afferent connections and laminar distribution of cells in the cat striate cortex. *J. comp. Neurol.* **187**, 725–744.

HENRY, G. H., LUND, J. S. & HARVEY, A. R. (1978). Cells of the striate cortex projecting to the Clare–Bishop area of the cat. *Brain Res.* **151**, 154–158.

HOFFMANN, K. P., STONE, J. & SHERMAN, S. M. (1972). Relay of receptive field properties in dorsal lateral geniculate nucleus of the cat. *J. Neurophysiol.* **35**, 518–531.

HOLLANDER, H. & VANEGAS, H. (1977). The projection from the lateral geniculate nucleus onto the visual cortex in the cat. A quantitative study with horseradish-peroxidase. *J. comp. Neurol.* **173**, 519–536.

HUBEL, D. H. & WIESEL, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *J. Physiol.* **160**, 105–154.

HUBEL, D. H. & WIESEL, T. N. (1965). Receptive fields and functional architecture in two nonstriate visual areas (18 and 19) of the cat. *J. Neurophysiol.* **28**, 229–289.

KATO, H., BISHOP, P. O. & ORBAN, G. A. (1978). Hypercomplex and the simple/complex cell classifications in the cat striate cortex. *J. Neurophysiol.* **41**, 1071–1095.

KENNEDY, H. & BALEYDIER, C. (1977). Direct projections from thalamic intralaminar nuclei to extra-striate visual cortex in the cat traced with horseradish peroxidase. *Expl Brain Res.* **28**, 133–139.

KRATZ, K. E., WEBB, S. V. & SHERMAN, S. M. (1978). Studies of the cat's medial interlaminar nucleus: a subdivision of the dorsal lateral geniculate nucleus. *J. comp. Neurol.* **181**, 601–614.

LEVAY, S. & FERSTER, D. (1977). Relay cell classes in the lateral geniculate nucleus of the cat and the effects of visual deprivation. *J. comp. Neurol.* **172**, 563–584.

LEVAY, S. & GILBERT, C. D. (1976). Laminar patterns of geniculocortical projection in the cat. *Brain Res.* **113**, 1–19.

LEVICK, W. R. (1972). Another tungsten microelectrode. *Med. & biol. Engng* **10**, 510–515.

LEVICK, W. R. (1977). Participation of brisk-transient retinal ganglion cells in binocular vision – an hypothesis. *Proc. Aust. Physiol. Pharmacol. Soc.* **8**, 9–16.

LEVICK, W. R., CLELAND, B. G. & DUBIN, M. W. (1972). Lateral geniculate neurons of cat: retinal inputs and physiology. *Invest. Ophthal.* **11**, 302–311.

MACIEWICZ, R. J. (1975). Thalamic afferents to areas 17, 18 and 19 of cat cortex traced with horseradish peroxidase. *Brain Res.* **84**, 308–312.

MOVSHON, J. A., THOMPSON, I. D. & TOLHURST, D. J. (1978). Spatial and temporal contrast sensitivity of neurones in areas 17 and 18 of the cat's visual cortex. *J. Physiol.* **283**, 101–120.

NIIMI, K. & SPRAGUE, J. M. (1970). Thalamo-cortical organization of the visual system in the cat. *J. comp. Neurol.* **138**, 219–250.

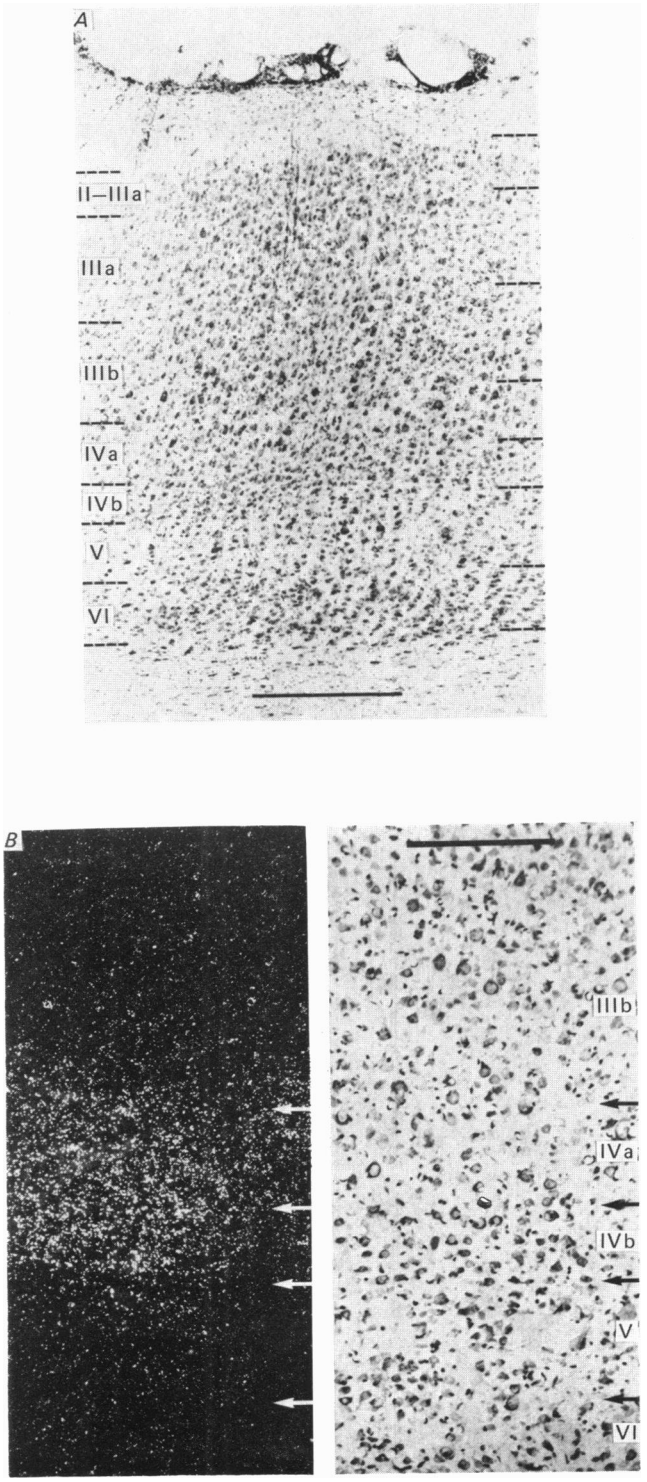
ORBAN, G. A. (1977). Area 18 of the cat: the first step in processing visual movement information. *Perception* **6**, 501–511.

ORBAN, G. A. & CALLENS, M. (1977). Receptive-field types of area 18 neurones in the cat. *Expl Brain Res.* **30**, 107–123.

OTSUKA, R. & HASSLER, R. (1962). Über Aufbau und Gliederung der corticalen Sehsphäre bei der Katze. *Arch. Psychiat. NervKrankh.* **203**, 212–234.

PALMER, L. A. & ROSENQUIST, A. C. (1974). Visual receptive fields of single striate cortical units projecting to the superior colliculus in the cat. *Brain Res.* **67**, 27–42.

ROSE, D. (1977). Responses of single units in cat visual cortex to moving bars of light as a function of bar length. *J. Physiol.* **271**, 1–23.



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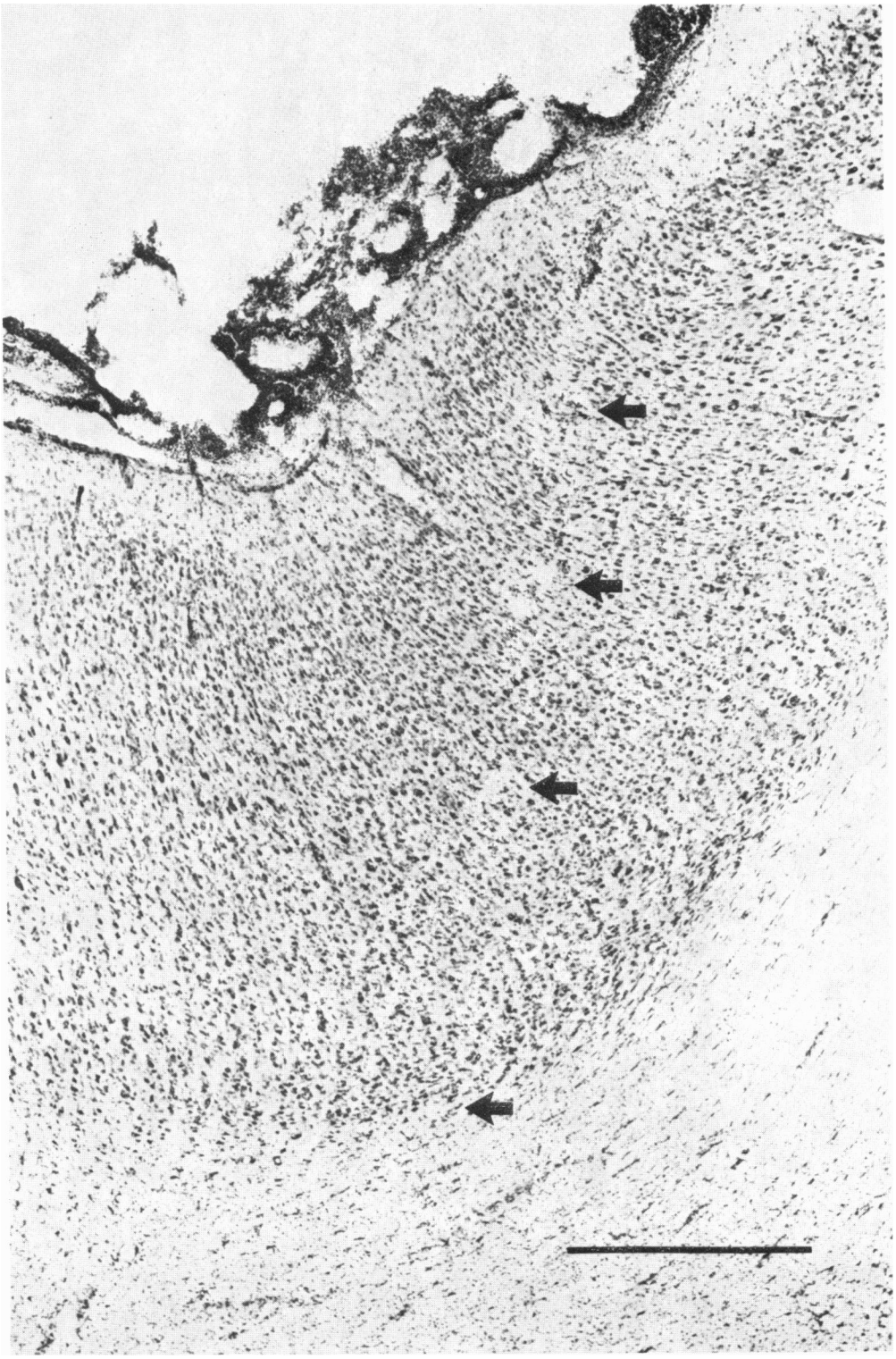

A. R. HARVEY

ROSENQUIST, A. C., EDWARDS, S. B. & PALMER, L. A. (1974). An autoradiographic study of the projections of the dorsal lateral geniculate nucleus and the posterior nucleus in the cat. *Brain Res.* **80**, 71–93.

SHERK, H. (1978). Area 18 cell responses in cat during reversible inactivation of area 17. *J. Neurophysiol.* **41**, 204–215.

SINGER, W. & BEDWORTH, N. (1973). Inhibitory interactions between X and Y units in the cat lateral geniculate nucleus. *Brain Res.* **49**, 291–307.

STONE, J. & DREHER, B. (1973). Projection of X- and Y-cells of the cat's lateral geniculate nucleus to areas 17 and 18 of visual cortex. *J. Neurophysiol.* **36**, 551–567.

TALBOT, S. A. (1942). A lateral localization in cat's visual cortex. *Fedn Proc.* **1**, 84.

TOLHURST, D. J. (1973). Separate channels for the analysis of the shape and the movement of a moving visual stimulus. *J. Physiol.* **231**, 385–402.

TOYAMA, K. & MATSUNAMI, K. (1968). Synaptic action of specific visual impulses upon cat's parastriate cortex. *Brain Res.* **10**, 473–476.

TOYAMA, K., MATSUNAMI, K., OHNO, T. & TOKASHIKI, S. (1974). An intracellular study of neuronal organization in the visual cortex. *Expl Brain Res.* **21**, 45–66.

TRETTER, F., CYNADER, M. & SINGER, W. (1975). Cat parastriate cortex: a primary or secondary visual area? *J. Neurophysiol.* **38**, 1099–1113.

VENES, J. L., COLLINS, W. F. & TAUB, A. (1971). Nitrous oxide: an anesthetic for experiments in cats. *Am. J. Physiol.* **220**, 2028–2031.

YAMANE, S., NIKARA, T. & SUGIE, N. (1977). Sustained and transient cortical neurones in area 18 of the cat. *Experentia* **33**, 477–479.

EXPLANATION OF PLATES

PLATE 1

A, photomicrograph of Nissl-stained section showing the disposition of laminae in area 18 of the cat. The area of cortex shown here comes from the lateral bank of the lateral gyrus. Scale marker, 500 μm. *B*, radioactive labelling in the parastriate cortex resulting from an injection of [^{3}H]proline into the d.l.g.n. Left, dark field photomicrograph showing distribution of silver grains; right, light field photomicrograph of same area showing laminar pattern. A dense band of labelling extends throughout laminae IVa and IVb. Scale marker, 200 μm.

PLATE 2

Photomicrograph of an electrode penetration in the lateral bank of the lateral gyrus. The track is entirely within area 18. Arrows show the positions of electrolytic lesions. The bottom lesion is more readily identified in an adjacent section. Scale marker, 1 mm.