AFFERENT AND EFFERENT CONNECTIONS OF THE CAT VISUAL CORTEX

by

A. R. Harvey

Department of Physiology
The John Curtin School of Medical Research
The Australian National University

Canberra

This thesis was submitted for the degree of
Doctor of Philosophy in the
Australian National University.

JULY, 1978

DECLARATION

The experiments described in this thesis are entirely my own work with the exception of some experiments reported in Chapters 1 and 4 which were performed in collaboration with Dr. G.H. Henry and Dr. J.S. Lund.

Alan Harvey.

A.R. HARVEY

As a result of work carried out during my tenure of a Research Scholarship in the Department of Physiology, the following papers have appeared or are to be submitted for publication.

Harvey, A.R. (1978). Characteristics of corticothalamic neurons in area 17 of the cat. *Neuroscience Letters*, 7, 177-181.

Henry, G.H., Lund, J.S. and Harvey, A.R. (1978). Cells of the striate cortex projecting to the Clare-Bishop area of the cat. *Brain Res.* (In press).

Lund, J.S., Henry, G.H., Macqueen, C.L. and Harvey, A.R. Anatomical organization of the primary visual cortex (area 17) of the cat. A comparison with area 17 of the Macaque monkey. (submitted to *J. comp. Neurol.*).

Harvey, A.R. The afferent connections and laminar distribution of cells in area 18 of the cat. (To be submitted to *J. Physiol. (Lond).*)

Harvey, A.R. The projections of areas 17 and 18 to the thalamus and superior colliculus of the cat. (To be submitted to *J. Physiol. (Lond).*)

Harvey, A.R. Interhemispheric visual connections of the cat. (To be submitted to *J. Physiol. (Lond).*)

Henry, G.H., Harvey, A.R. and Lund J.S. The afferent connections and laminar distribution of cells in the cat striate cortex. (To be submitted to *J. comp. Neurol.*)

ACKNOWLEDGEMENTS

I wish to thank my supervisor, Professor P.O. Bishop, F.R.S., for his assistance and advice during my tenure of a Research Scholarship at the Australian National University. I would also like to acknowledge the encouragement and guidance of Dr. G.H. Henry.

I would like to acknowledge the support of Mr. L.M. Davies and Mr. R.M. Tupper and members of the technical staff, in particular, Mr. C.L. Macqueen (for help with histological preparations) and Mr. K. Collins (for assistance in the preparation of the experiments and in helping prepare the figures). I am also grateful for the help of Mr. R. Westen and the staff of the Photographic Unit

Finally, I wish to thank Ms. J. Livingstone for her secretarial assistance and Ms. J.M. Anderson for her indefatigable labours during the typing of this thesis.

TABLE OF CONTENTS

GENERAL INTRODUCTION

Until the early part of the nineteenth century it was widely believed that the centre of sensation and perceptual processing in the brain lay within the thalamus and midbrain, while the function of the overlying cerebral hemispheres presented something of a mystery. The pioneering experiments of Fluorens (1842) showed however, that removal of parts of the cortex (while leaving the lower cerebral tissue intact) severely altered the behaviour of pigeons and chickens and he concluded that the intellectual faculties, the "will", and the sensory performance of "perception" were localized in the cerebral hemispheres . Of specific importance was his observation that unilateral destruction of the cortex resulted in a permanent loss of sight in the contralateral eye. Later, Munk (e.g. 1890) showed that a localized area of the cortex of the occipital lobe was essential for vision in the dog and monkey and Henschen (1893) reached the same conclusion from a clinicopathological examination of human brains.

The concept that particular areas of the cortex were concerned with specific functional tasks was supported by the work of Fleschig (cf. Clarke and O'Malley, 1968) who observed that the myelination of nerve fibres occurred initially in the pathways arising from the sense organ (the primary pathway) and only later in pathways linking one cortical area to another. He found five primary regions or sensory centres in each cerebral hemisphere corresponding to the principal afferent fibre tracts which arise from the various sense organs.

However these regions made up less than one-third of the entire cortex. The remainder of the cortical surface he described as comprising secondary or association areas. These regions did not have direct access to incoming sensory information but were involved in the elaboration of higher and more intellectual functions including memory and the integration of sensory information in order to perform complex behavioural acts.

With the realisation of the crucial role that the cortex played in higher cerebral functions, anatomists began to look more closely at its fine structure. The first to have noticed any local variation in cortical architecture was Gennari (cf. Polyak, 1957) who observed a white line which was most readily visible in the occipital lobe. This work was further expanded by Baillager (1840) and Remak (1844) who maintained that, as one proceeded from the pia to the underlying white matter, the cortex could be subdivided into a maximum of six parallel layers.

The advent of better fixation and staining techniques allowed a more detailed study of the intrinsic architecture of the grey matter of cerebral cortex and it was now possible from the variations in cellular patterns in histological sections to recognise different cortical regions. Nissl stains, which stain the cell bodies, were used by both Campbell (1904) and Brodmann (1909) to map cytoarchitectural subdivision of the cortex. Brodmann (1909) identified 52 such subdivisions in the cerebral cortex and agreed that the cortex could be subdivided into six layers, the relative dimensions of each lamina varying in different cortical regions. Campbell (1904), and later Economo (1929), recognised five basic types of cortical

organization based on an examination of the cytoarchitecture of the various areas. In this work it was recognised that in motor cortex, lamina V and VI were well developed (agranular cortex) whereas in sensory areas lamina IV was preeminent (granular cortex). From these studies, basic principles were developed in relating functional performance to the laminar pattern in cerebral cortex. Briefly lamina IV was regarded as the receiving lamina, laminae I, II and III were the correlating laminae interpreting information arriving at lamina IV, and laminae V and VI were the motor or efferent layers acting on information received and interpreted in the outer layers.

More recently, a number of histological techniques have been developed for tracing the nerve pathways linking the various parts of the central nervous system. These include:

A. *Degeneration of nerve terminals*. Following damage of a cell body, its axon terminals degenerate and may be revealed by a reduced silver staining technique.

B. *Orthograde transport of radioactive metabolites to nerve terminals (autoradiography)*. After radioactively labelled metabolites are injected around a cell body, they are taken up and transported to the axon terminals. The location of these metabolites can be shown by developing histological sections previously coated with photographic emulsion.

C. *Retrograde transport of horseradish peroxidase*. When injected around nerve terminals, this enzyme is retrogradely transported back along the axon to the cell body where its

presence may be revealed with histological stains. This technique enables the precise location of the efferent cell body to be determined.

In the visual system, these techniques have been used to great effect in studying the connectivity between one region and another. It is inappropriate in this introduction to give a detailed account of the results obtained using these methods and a more comprehensive analysis is presented in the relevant chapters that follow. In outline, these techniques have shown that lamina IV in both the striate (area 17) and parastriate (area 18) cortex receives most of the primary projection from the lateral geniculate nucleus. Efferent cells, projecting subcortically are located in laminae V and VI and appear to have a pyramidal morphology. Efferent cells are also found in laminae II and III but these send axons to other cortical regions and may be regarded as an extension of the correlation of visual information which occurs within any given cortical area.

Broadly speaking, the neurohistological concepts that prevailed early in the present century have provided a sound basis for the interpretation of information processing in the cortex. More modern neuroanatomical techniques have experimentally confirmed many of the early proposals regarding the intrinsic organization of cortical areas and have extended this work by describing the origin and destination of afferent and efferent pathways which enter or leave the cortex. Given the wealth of anatomical data now available, the way is open for a physiological analysis of the functional properties of

these intrinsic and extrinsic cortical pathways. Such an analysis is undertaken in this thesis. Experiments have been mostly confined to an examination of the afferent and efferent connections of two visual cortical areas (areas 17 and 18) in the occipital lobe of the cat. The functional elaboration that takes place in the early stages of the processing of incoming visual information has been examined. In addition it has proved possible to determine the stage that functional organization has reached prior to projection to extrinsic sites.

SYNOPSIS OF STUDY

If, as suggested by the anatomy, different cortical laminae perform different functions, it might be expected that this segregation would be reflected in the response properties of cortical cells. As a first step therefore, the laminar distributions of the various types of striate and parastriate neurons (defined by their response to visual stimulation) are examined. These results are discussed in Chapters 1 and 2.

An analysis of the laminar distribution of functional cell types, in itself however, provides only indirect evidence concerning the nature of cortical processing. In order to study the connectivity of visual neurons more directly, their afferent input has been examined using electrical stimulation techniques. To this end, stimulating electrodes were placed in the optic chiasm and optic radiation and the afferent connectivity of striate and parastriate neurons has been

compared to their visual receptive field properties and their laminar distribution. Consistent with anatomical studies, the physiological analysis indicates that incoming visual information is received in lamina IV (and to some extent in lamina VI) and is then relayed to more superficial layers and to lamina V.

The efferent connectivity of the striate and parastriate cortex is examined in Chapters 3, 4 and 5. Stimulating electrodes were placed in a number of cortical and subcortical sites; the superior colliculus, the ipsilateral Clare-Bishop cortex, the corpus callosum, the contralateral visual cortex and in or close to the lateral geniculate nucleus. The studies confirm that subcortically projecting neurons are confined to the deeper layers (laminae V and VI) while cells efferent to other cortical regions are located in lamina III. The visual properties of the various types of efferent neuron have been examined and the results are discussed with regard to the functional significance of the subcortical and cortico-cortical projections.

In addition, the afferent connections of efferent neurons have been examined in order to study the input-output relations of areas 17 and 18. The results indicate that the input to cells projecting out of the cortex does not necessarily pass through the correlating laminae (II and III) and shows that some efferent neurons are monosynaptically excited by geniculocortical afferents.

CHAPTER ONE

THE AFFERENT CONNECTIONS AND LAMINAR DISTRIBUTION OF CELLS IN AREA 17

INTRODUCTION

Area 17 of the cat has been the subject of a great deal of intensive physiological research over the past 15 to 20 years. In general terms, a large proportion of this work has been directed towards an understanding of how incoming visual information is elaborated and processed within the striate cortex. Hubel and Wiesel (1962), the pioneers in this field, concluded that neural signals progressed through a heirarchical sequence in which each cell received afferents from two or more neurons in the preceding stage. From an analysis of the receptive field properties and laminar distribution of striate neurons, Hubel and Wiesel (1962) suggested that geniculocortical fibres innervated simple cells which in turn provided the input to cells with complex receptive fields. In a later study, Hubel and Wiesel (1965) extended this heirarchical concept by proposing that complex cells were afferent to the hypercomplex cells encountered in areas 18 and 19. Subsequently it has become clear that hypercomplex cells also exist in the striate cortex (Dreher, 1972; Bishop and Henry, 1972; Kelly and Van Essen, 1974; Wilson and Sherman, 1976; Camarda and Rizzolatti, 1976a; Gilbert, 1977; Sillito, 1977a,b; Sillito and Versiani, 1977; Henry, Lund and Harvey, 1978; Kato, Bishop and Orban, 1978) but this discovery does not invalidate the heirarchical scheme of Hubel and Wiesel.

The concept of serial processing within the visual cortex has been pervasive throughout the literature for many years. However, recent studies which have examined the responses of

cells to electrical stimulation of the primary visual pathway have cast serious doubts on the validity of Hubel and Wiesel's proposal. Specifically it has been shown that after stimulation of the optic chiasm (OX) or optic radiation (OR), the latencies of many complex cells are shorter than the earliest simple cell response (Hoffmann and Stone, 1971; Stone and Dreher, 1973; Singer, Tretter and Cynader, 1975). Obviously such a result is not consistent with the heirarchical concept that complex cells derive their input solely from simple cells.

The situation becomes even more complicated when consideration is given to the observation that there is more than one stream of information being transmitted to the striate cortex from the dorsal lateral geniculate nucleus (dLGN). Anatomical studies have shown that both large and small geniculate neurons project to area 17 (Garey and Powell, 1967, 1971; Gilbert and Kelly, 1975; Laemle, 1975; Garey and Blakemore, 1977; Hollander and Vanegas, 1977; Kennedy and Baleydier, 1977; LeVay and Ferster, 1977). These geniculate cells are likely to be Y and X respectively (e.g. LeVay and Ferster, 1977) and consistent with this, Stone and Dreher (1973) were able to activate both types of neuron at low thresholds after electrical stimulation of the striate cortex. In addition, the W cell (Wilson, Stone and Sherman, 1976) and the sluggish and non-concentric geniculate neurons (Cleland, Levick, Morstyn and Wagner, 1976) may also project to area 17.

Are these streams kept separate in the cortex or do they converge onto single striate neurons? On the basis of the orthodromic OX and OR latencies of cells in area 17, Hoffmann

and Stone (1971) and Stone and Dreher (1973) suggested that simple and complex cells were innervated by X and Y geniculate cells respectively. They proposed that afferent information is processed in parallel rather than serially in the striate cortex. Singer *et al.* (1975) also found little evidence for serial elaboration within area 17 although their results differed in that both simple and complex cells could be driven by either X- or Y-type afferents. Singer *et al.* (1975) concluded that parallel processing did occur but that it was reflected in the simple/complex dichotomy rather than in the distinction between X and Y streams.

Although the electrical stimulation studies described above reach the same general conclusion, there are clearly some important differences with respect to specific details about the afferent connectivity of striate neurons. Furthermore, none of the earlier studies have examined the laminar distribution of the different types of cell within area 17. Geniculocortical fibres terminate mostly in lamina IV but also to some extent in lamina VI of the striate cortex. (Colonnier and Rossignol, 1969; Rosenquist, Edwards and Palmer, 1974; LeVay and Gilbert, 1976). It might be expected therefore that monosynaptically activated cells would be found most commonly in these two layers. In this regard it is somewhat paradoxical that both simple and complex cells are directly innervated by geniculate axons yet simple cells are by far the commonest cell type encountered in lamina IV (Hubel and Wiesel, 1962; Kelly and Van Essen, 1974; Gilbert, 1977; Sillito, 1977a; Kato, Bishop and Orban, 1978).

In an attempt to clarify some of the problems outlined in

the foregoing, the present study combines a laminar analysis with an examination of the afferent connectivity of striate neurons. The general receptive field properties and laminar disposition of the various striate receptive field classes are considered in the first part of the analysis. In the second part the afferent connections of cells in area 17 are correlated with the neurons' receptive field properties and laminar position. Special attention was given to a study of the OX-OR latencies and visual properties of geniculocortical axons recorded within the grey matter of the cortex. Information about the response latencies of different classes of geniculate afferents proved an important aid in the assessment of the type of fibre innervating striate neurons.

METHODS

The general experiment techniques described below have been employed in all of the physiological studies presented in this thesis.

Cats (weight range 2.5 to 4.0 kg) were anaesthetised with a halothane (induced on 4%, maintained on 1-1.5%) and 70% N_2O/30% O_2 mixture for the surgical procedures. A trachael cannula was inserted which contained a specially designed inner sleeve to allow free passage of the gas mixture. This inner sleeve could be withdrawn at any time to remove mucus which often collected at the base of the cannula. The animal's temperature was maintained at 38° by an electric heating blanket controlled by a thermistor placed under the scapula. Pressure on the thorax was reduced by suspending the animal from a spinal clamp. Eye movements were reduced to a very low level by paralysis of the animal and by bilateral cervical sympathectomy. Paralysis was induced by an initial intravenous injection of 40 mg gallamine triethiodide (Flaxedil; May and Baker) and was maintained by a continuous intravenous 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).

Long lasting local anaesthetic (Marcain; Astra) was infused into all wound margins after completion of the surgery, as was Neosporin (Calmic Pharmaceuticals) a topical antibiotic powder. After paralysis and during recording, animals were artificially respired with a 70% N_2O/30% O_2 mixture usually at a rate of 25

strokes per minute. Stroke volume varied from about 40-50 ml per stroke depending on the size of the cat. Daily, 0.2 ml of an antibiotic, triplopen (Glaxovet) was injected intramuscularly into the cat and occasionally 2.5 mg hydrocortisyl (Roussel) was similarly administered.

The corneas were protected with plastic contact lenses of zero power and the eyelids and nictitating membranes were retracted with neosynephrine (Winthrop) (2.5%). A drop of Neosporin ophthalmic solution(Calmic Pharmaceuticals) was placed on each eye and the pupils were dilated with atropine (Sigma) (1%). An indirect ophthalmoscope (Fundus Camera, Carl Zeiss, Oberkochen/Wuertt) was used for projecting retinal landmarks. Artificial pupils (3 mm in diameter) were centred on the area centralis using the modified viewing system of the fundus camera (Bishop, Henry and Smith, 1971). A slit retinoscope (Hamblin) was used to refract the cat for a viewing distance of one metre 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 were performed for the insertion of the recording and stimulating electrodes. The dura was removed at all of these sites. For recording, a tungsten in glass microelectrode (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, Henry and Smith, 1971). The recording electrode was driven down until contact was made with the cortex. This was recognized by

a sudden increase in the background noise level followed, usually within 100-200μ, by a cell death. Thence forward, the electrode was advanced at 1μ steps using an electrically driven Kopf microdrive. Conventional differential amplification and filtering (band pass : 60 Hz to 6000 Hz) were used to record the activity of single neurons isolated by the electrode. Extracellularly recorded action potentials were monitored both auditorily on an audio amplifier and visually on a cathode ray oscilloscope (Tektronix Dual Beam RM565).

The stereotaxic head holder used in these experiments was similar to that described by Bishop, Kozak, Levick and 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, Henry and Smith, 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 receptive fields 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 inches in diameter; 80% platinum, 20% iridium) insulated with glass. The exposed tip normally protruded about 1 mm from the end of the insulation. Electrical pulses (50-200μs) were generated either by a System of Neurolog (0-10mA) or Tektronix (0-100 volts) pulse and waveform

generators. The stimulating electrodes were isolated using an Ortec Isolator. Bipolar stimulating electrodes were always used and current was passed between pairs of electrodes. Photographic records of electrical stimulation were obtained using a Grass camera and latencies were checked by projecting the film through a Leitz 1C 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 and Davis (1962) and are described more fully in Chapter 3.

In the experiments described in this chapter, a pair of electrodes were placed in the optic radiation (OR) of 34 cats (anterior 6 mm, lateral 8 and 10 mm, depth about 10 mm) and in the optic chiasm (OX) of 19 of these animals (anterior 15 to 16 mm, lateral 1.5 mm, depth about 23-24 mm). The two pairs of electrodes were placed stereotaxically, but field potentials recorded in area 17 were used to check that the electrodes were at the optimal depth. The stimulating electrodes were not included in the sealed chamber of the recording electrode, but their craniotomies were covered with a protective layer of agar.

Electrolytic lesions (5μA/5-7 secs, tip negative) were made at various points during the recording penetration. After the experiment, the animal was intravenously injected with Nembutal (Abbot Laboratories), and perfused through the heart with 10% formal saline. Nissl-stained frozen sections (40μ) 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 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.

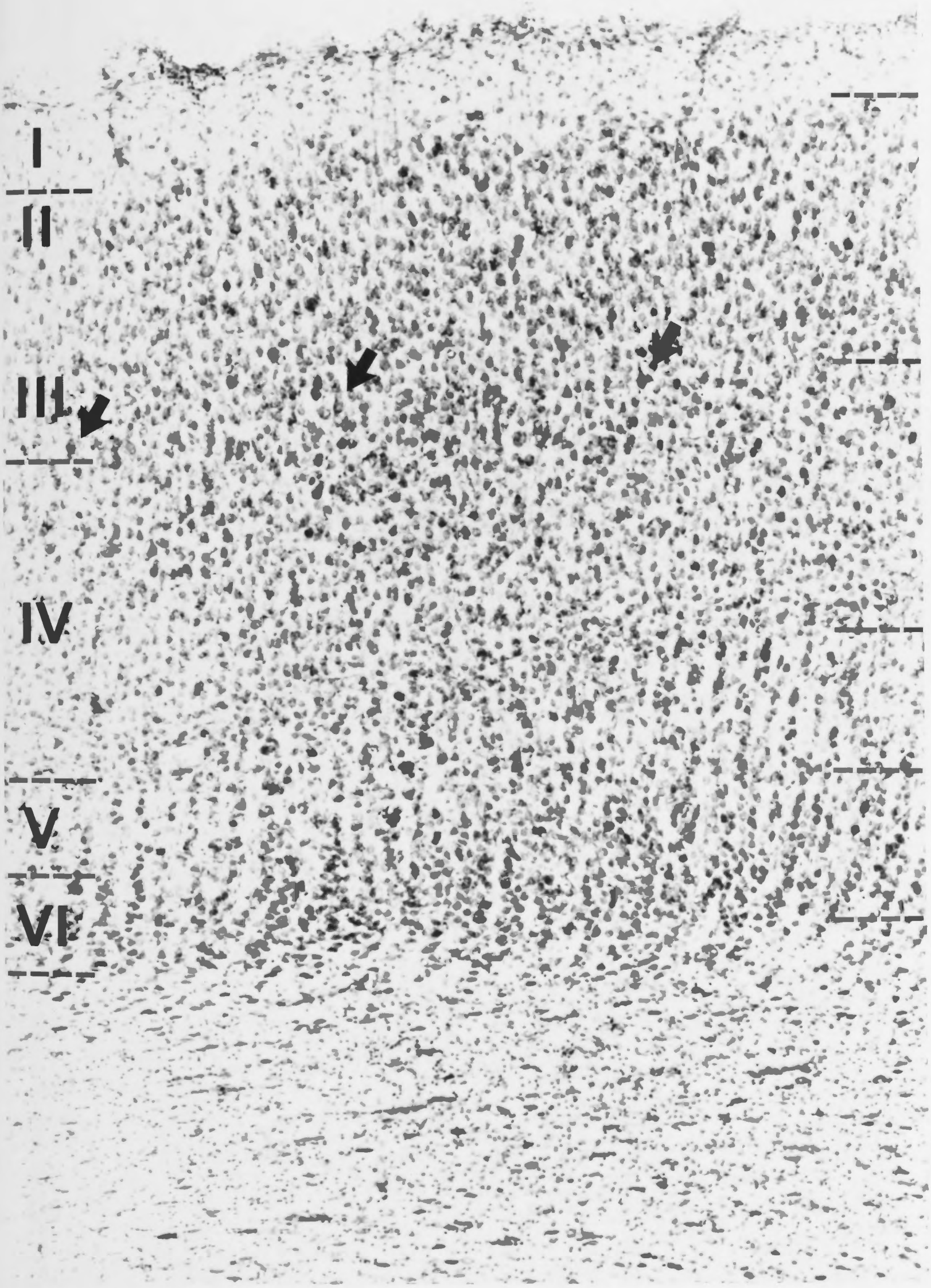
In one adult cat, (^{3}H) proline was injected under pressure through a micropipette into the dLGN. The injection delivered 1 µL of 10 µCi (^{3}H) proline. After 24 hours survival, the animal was anaesthetised with Nembutal and perfused through the heart with lite fix (neutral buffered paraformaldehyde). The blocks of brain were allowed to fix for several hours and were then placed to sink in 30% sucrose solution in 0.1 m phosphate buffer. Frozen sections 40 µm thick were dipped in Nuclear Tract emulsion NTB2 (Kodak), exposed to the radiation for 6 weeks and then developed in D19 developer (Kodak) and fixed with Kodak rapid fixer. The sections were lightly counter stained with cresyl violet.

Scheme of Cortical Lamination

The interpretation of the present results is critically dependent on an unambiguous understanding of the disposition of laminae in the cat striate cortex. The scheme of lamination adopted in the present study is based on that of O'Leary (1941). An example of a Nissl-stained section of area 17 is shown in Fig. 1.

Lamina I: In Nissl preparations, lamina I is observed as a cell free zone immediately beneath the pial surface. Although O'Leary (1941) found occasional cell bodies in lamina I, the

Fig. 1. Photomicrograph of Nissl-stained section showing the disposition of laminae in cat striate cortex. The area of cortex shown here was taken from the medial bank of the lateral gyrus, above the suprasplenial sulcus. Arrows indicate the position of large border pyramids (O'Leary, 1941).


I
II
III
IV
V
VI

zone is composed principally of the terminal arborizations of the apical dendrites of underlying pyramidal cells and the afferent axon terminals of cells in the thalamus and extra-striate cortical regions.

Lamina II: The junction between lamina II and III is difficult to identify in Nissl material. Commonly considered to be 7 or 8 cell bodies thick, lamina II comprises mainly smaller, less intensely staining pyramids than in the underlying lamina III.

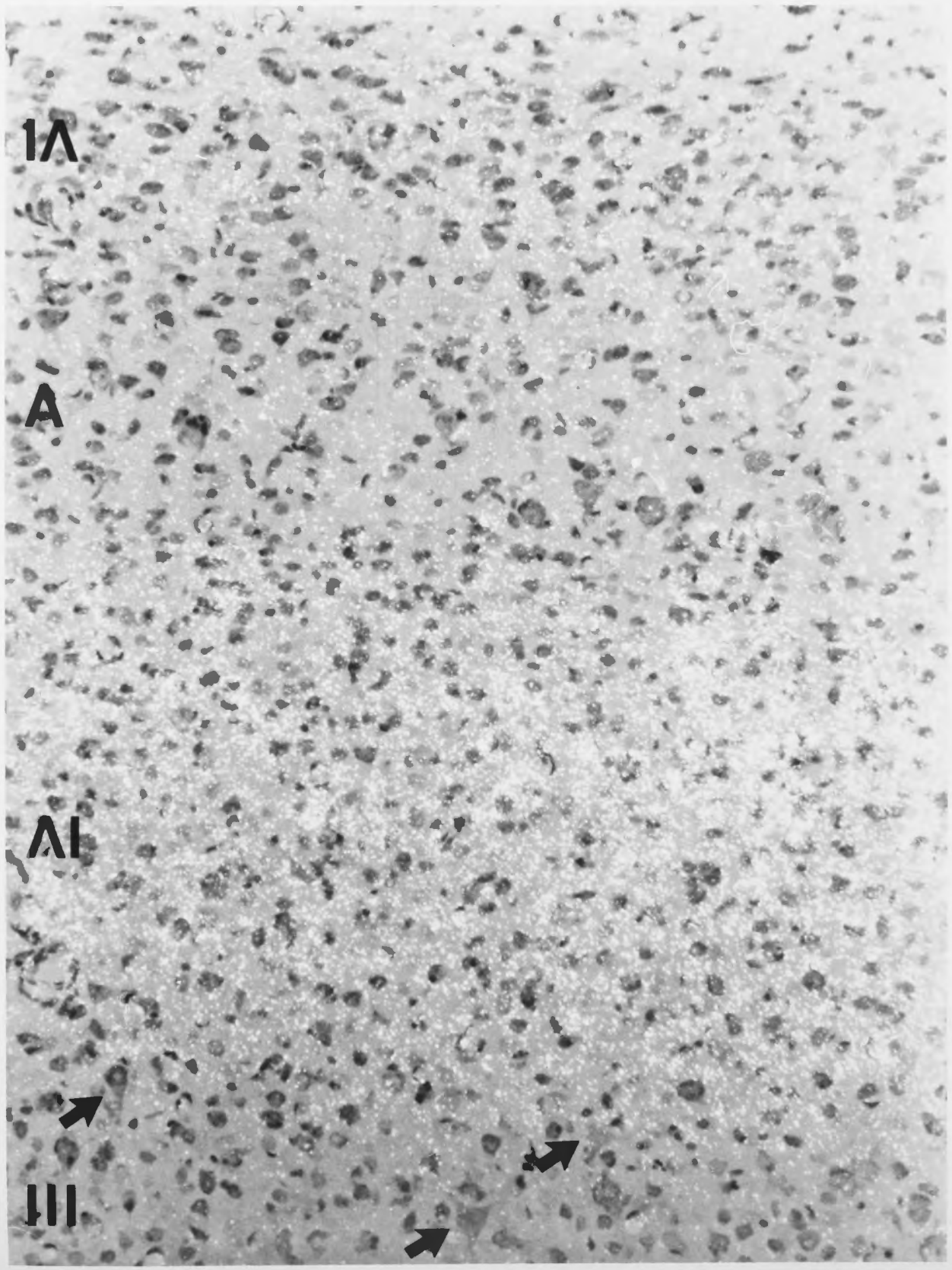
Lamina III: Lamina III, like lamina II, is composed principally of small pyramidal cells although the proportion of pyramids with larger cell bodies increases in the deeper reaches of the lamina.

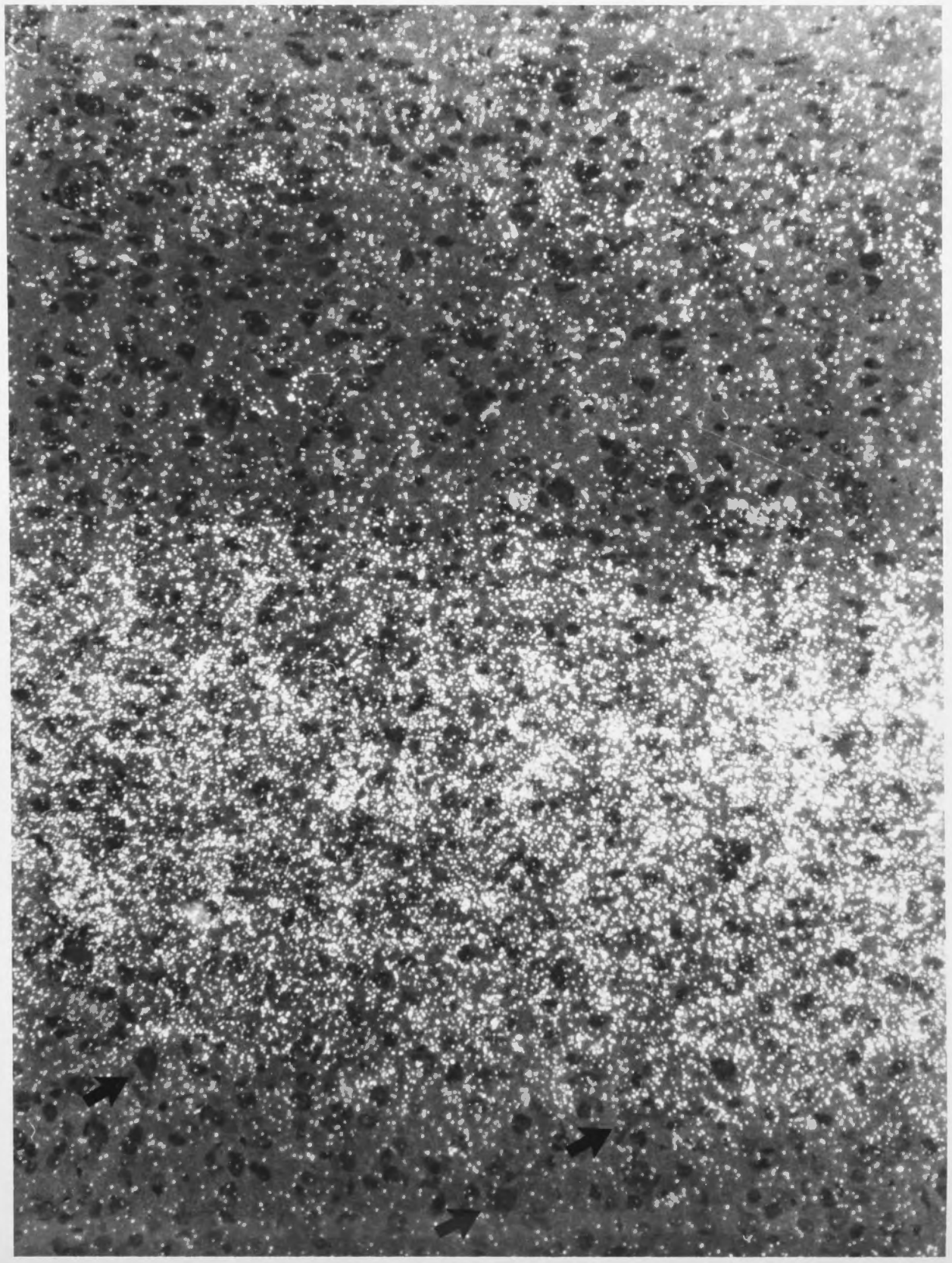
The III/IV border: The border between laminae III and IV is the subject of considerable interpretative variation. Classically, the upper margin of layer IV was identified as corresponding with the upper boundary of the stria of Gennari but the problem of locating the stria is not easily resolved in the cat cortex. From observations of Nissl preparations of 14 day old kitten cortex, Brodmann (1909) concluded that the upper margins of the stria of Gennari and laminar IVB were coincident in the cat and that the lamina corresponding to IVA of the primate was either absent or combined with lamina IVB. Brodmann (1909) considered that upper lamina IVB, while predominantly composed of large stellate cells, also contained some larger pyramidal cells. Later, O'Leary (1941) from Golgi material decided that upper lamina IV contained only small pyramids (the star pyramids of Lorente de Nó, recognised from an apical dendrite that put off branches close

to the soma but otherwise remained unbranched) and he placed the large, or border pyramids at the lower margin of lamina III.

Recently, the extent of lamina IV in the primate has been delineated from the presence of spiny stellate cells. More specifically, spiny stellates are found in lamina IVA above moderately sized pyramids present in lamina IVB (Lund, 1973). In Golgi preparations of the cat striate cortex (Lund, Henry, Macqueen and Harvey, in preparation), no spiny stellate neurons are found lying level with or above the border pyramids of O'Leary. The interpretation of the III/IV border seems to involve a decision as to whether it is the equivalent of the primate lamina IVA or lamina IVB that is absent from the cat cortex. If lamina IVA is absent, then the cat border pyramidal neurons could be correlated with the pyramids of lamina IVB in monkey. However, both the spiny stellates and the pyramids in lamina IVB in the primate send axons out of the striate cortex to terminate in the cortex of the superior temporal sulcus, (Lund, Lund, Hendrickson, Bunt and Fuchs, 1975) a region that has no obvious analogue in the cat. It is also significant that a stria of white matter in lamina IVB of the primate, which arises from the cortex of the superior temporal sulcus, is not apparent in the cat cortex. If an equivalent to the primate lamina IVB is absent from the cat, then cells with extrinsic axons projecting to extra-striate cortical regions would logically be placed in lamina III (or lamina II) and reinforce O'Leary's decision to include the border pyramids in lamina III. In this regard, there is evidence that the axons of border pyramids show sites of destination in common with the

Fig. 2. Radioactive labelling in area 17 resulting from injection of (^{3}H) proline into the dorsal lateral geniculate nucleus. Each photomicrograph consists of both a light and a dark field exposure. Left, dark field exposure predominates; right, light field exposure (of the same area) predominates. Labelling is confined to laminae IV and VI. Arrows indicate the location of large pyramidal cells at the border between laminae III and IV (see text).


1A
A
IV
III



pyramids in the body of laminae II and III. Thus the border pyramids along with the pyramids of laminae II and III are labelled when horseradish peroxidase is injected into the Clare-Bishop cortex (Lund, Henry and Bullier, unpublished).

The considerations presented above suggest therefore, that the border between laminae III and IV should be placed at the level of the border pyramids of O'Leary (1941). Support for this proposition comes from an examination of the labelling in the striate cortex after a bilateral injection of (^{3}H) proline into laminae A and A1 of the dLGN.

The laminar distribution of (^{3}H) proline in the striate cortex is shown in Fig. 2. Clearly, the density of silver grains falls off abruptly just above the large pyramids in lamina V and, more importantly, does not extend to any significant degree beyond the border pyramids at the presumed laminae III/IV border. This observation is consistent with the proposition that the border pyramids are at the lower margin of lamina III (O'Leary, 1941) and this is the scheme adopted here. By comparison, there is little doubt that Otsuka and Hassler (1962) included these pyramids in lamina IV.

Lamina IV: In O'Leary's scheme lamina IV is subdivided into layers IVA and IVB on the basis of cell size in both Nissl and Golgi preparations; lamina IVB has smaller and less deeply staining stellate cells than lamina IVA (cf. Garey, 1971). Small pyramids are observed in both IVA and IVB but only the star pyramid is found in IVA.

Lamina V: From the majority of lamination schemes lamina V is

readily identified from the presence of the largest pyramidal cells to be found in the striate cortex. However there is some uncertainty about the location of the upper border of lamina V. O'Leary (1941) suggested that a discrete sub lamina - VA - exists between the lower margin of lamina IVB and the upper edge of lamina VB with its large pyramids. As is common to lamina V, O'Leary observed pyramids in lamina VA with recurrent axons, but stressed the difficulty of recognising this lamina in Nissl preparations since these cells are gathered in irregular clusters which invade the boundaries of both IVB and VB.

Lamina VI: As pointed out by Otsuka and Hassler (1962), the cells of lamina VI, in contrast to those of lamina V which are irregularly distributed, are arranged in columns in the direction of the radiating fibres. The thickness of lamina VI varies according to surface topography becoming very narrow in the base of sulci and greatly expanded in gyral convexities. With Cresyl violet the cells of lamina VI stain more heavily than those of lamina V.

The conditioning technique

After OX stimulation, it is widely agreed that X cells in the lateral geniculate nucleus are less easily activated than Y cells (Stone and Hoffmann, 1971; Hoffmann, Stone and Dreher, 1972; Singer and Bedworth, 1973; Stone and Dreher, 1973). This observation appears to be due to the fact that disynaptic inhibition mediated by the fast conducting Y system prevents the more slowly conducting retinal fibres that innervate X cells from eliciting action potentials. Similarly, cells in the visual

cortex innervated by slowly conducting or X-type dLGN fibres are more difficult to excite from the optic radiation than are cells which receive a fast input (Stone and Dreher, 1973; Singer, Tretter and Cynader, 1975). Again this is related to the observation that cells driven by fast fibres inhibit cells which are innervated by more slowly conducting afferents. Excitatory post synaptic potentials are seen, but they do not reach a threshold sufficient for initiation of an impulse due to the hyperpolarising action of the preceding inhibitory post synaptic potentials (Singer *et al.*, 1975).

Consistent with the observation that many X cells are afferent to area 17 (see INTRODUCTION), it was often difficult to electrically excite striate neurons in the present study. Activation was especially difficult from the optic chiasm, presumably because there are two stages (the dLGN and the cortex) where inhibitory interactions can occur. This convergence of inhibitory and excitatory pathways therefore poses a number of problems when extracellular recording techniques are used. A method was discovered however, which significantly increased the probability of excitation of striate neurons. It was found that stimulation of the OX or OR often elicited a response only if a spontaneous or visually evoked spike (called the conditioning spike) *preceded* the electrical shock.

The experiment was arranged so that electrical stimulation could not occur unless it was triggered by an action potential (whether of visual or spontaneous origin) generated in the cell being studied. The procedure is therefore identical to that used in the collision test (see Chapter 3). By varying the

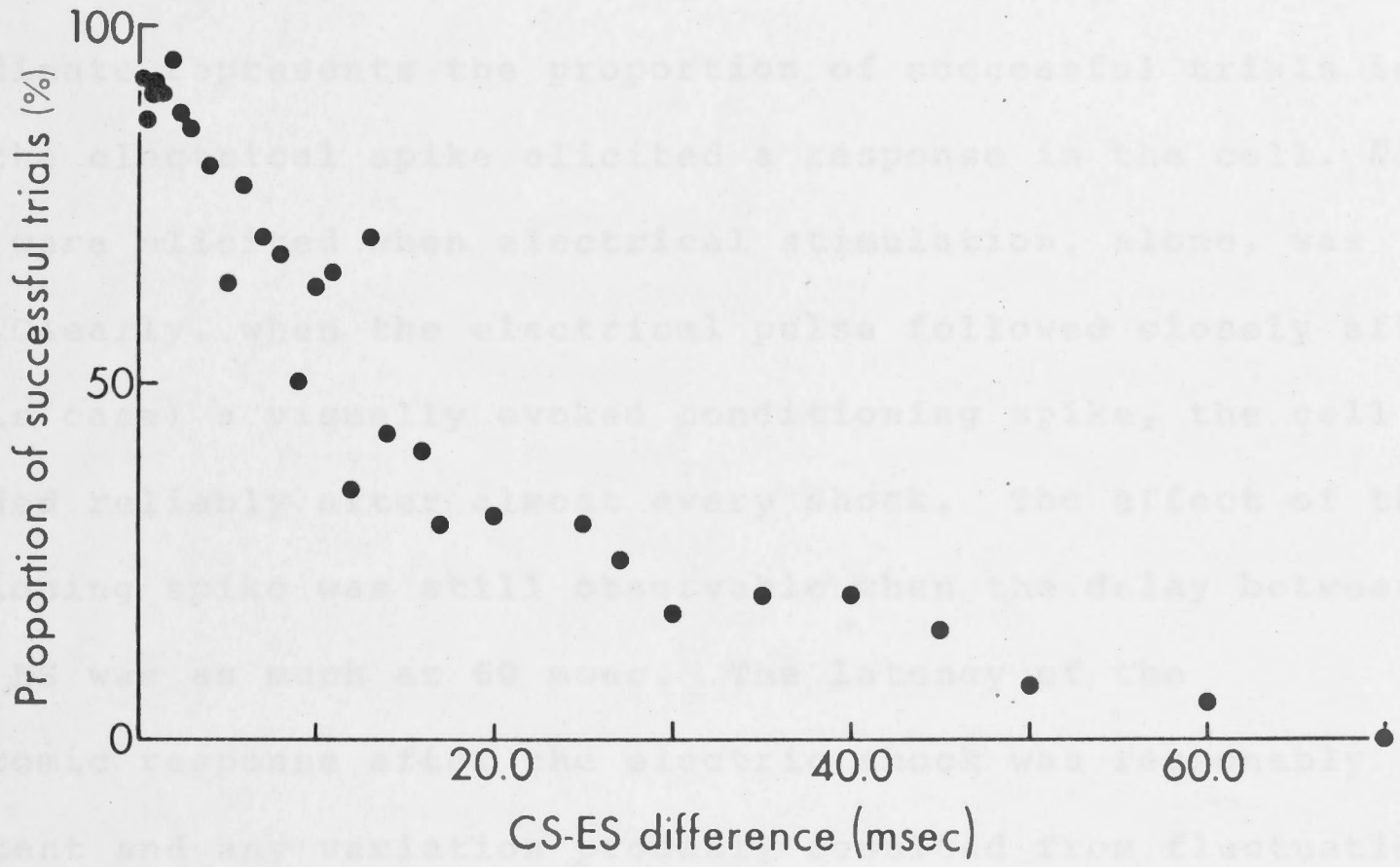


Fig. 3. Time course of the conditioning effect in a striate neuron. The ordinate indicates the proportion of trials in which electrical stimulation elicited an orthodromic response. CS-ES difference, the time delay between the visually evoked conditioning spike (CS) and the electrical shock (ES). No orthodromic spikes were elicited when electrical stimulation, alone, was used.

delay between the conditioning spike (CS) and the electrical stimulation (ES) it was possible to study the time course of the conditioning effect. An example is shown in Fig. 3. A total of 40 trials were made for each CS-ES time difference. The ordinate represents the proportion of successful trials in which the electrical spike elicited a response in the cell. *No* spikes were elicited when electrical stimulation, alone, was used. Clearly, when the electrical pulse followed closely after (in this case) a visually evoked conditioning spike, the cell responded reliably after almost every shock. The effect of the conditioning spike was still observable when the delay between CS and ES was as much as 60 msec. The latency of the orthodromic response after the electric shock was reasonably consistent and any variation probably resulted from fluctuations in the synaptic transmission delay.

The orthodromic OR latency of the striate cell shown in Fig. 3 was 1.9 ±0.1 msec which suggests that the cell was innervated by a relatively slow afferent fibre. In all, 42 cells which did not respond to electrical stimulation alone could be excited using this technique. The time course of the effect was measured on 5 striate cells and in all cases the conditioning spike still enhanced the cell's response to electrical stimulation at CS-ES differences of 50 msec or more. The physiological mechanism underlying this phenomenon is not completely clear. Interestingly, enhancement of the orthodromic response does not occur if an electric shock is employed as the conditioning stimulus. It may be that the more specific visual or spontaneous spike in some way prevents the Y-mediated

inhibition (Singer *et al.*, 1975) from exerting its influence, perhaps by some form of inhibition of the interneuron.

RESULTS

General Comments

The units recorded in this study were isolated in 64 electrode penetrations in 39 cats. In all, 882 units were held for long enough to allow a thorough examination of response properties. However, some of these units were so unresponsive to visual stimuli that their receptive field remained unclassified. Also it was not always possible to be sure of the laminar position of a cell in the histological reconstruction of the electrode track. Of the 882 isolated units, 347 were rejected because their cortical location was too uncertain and of the remaining 535 units, 364 (68%) responsed to visual stimuli sufficiently well for them to be classified by their receptive field properties. The receptive fields of striate neurons were classified by their response to hand-held stimuli.

RECEPTIVE FIELD CLASSIFICATION

Table 1 provides a summary of the criteria used for differentiating one cell type from another. The nomenclature adopted in this study has been described previously (Henry, 1977) and briefly the S cell has properties similar to the simple cell, the C cell is similar to the complex cell with uniform receptive field (Hubel and Wiesel, 1962) and the subscript H specifies the presence of the hypercomplex property. The B cell (Henry, Lund and Harvey, 1978) shares the C cell's response to a flashing stimulus (that of composite ON/OFF discharge) but differs from the C cell in a number of important aspects that are summarized in Table 1. The hypercomplex property may also be present in

TABLE 1

Receptive field classification of striate neurons

	S	C	B
RESPONSE TO FLASHING BARS (i) CHARACTER *(ii) DIMENSION (iii) DURATION	Areas of ON or OFF discharge <1° wide; <1° long Sustained or transient	Area of composite ON/OFF discharge >1° wide; >2° long Usually transient	Area of composite ON/OFF discharge <2° wide; <2° long Usually sustained
RESPONSE TO LIGHT AND DARK MOVING EDGES (i) CHARACTER (ii) LOCATION *(iii) DIMENSION (iv) RESPONSE PROFILE * Min response field	Discharged by light and/or dark edges Discharge areas spatially displaced <1° wide; <1° long SMOOTH	Discharged by light and dark edges Discharge areas spatially coincident >2° wide; >2° long UNEVEN	Discharged by light and dark edges Discharge areas spatially coincident <2° wide; <2° long SMOOTH
SPONTANEOUS ACTIVITY	NIL OR LOW	MODERATE (GENERALLY FROM 5 TO 20 SPIKES/SEC)	NIL OR LOW
DIRECTION SELECTIVITY	When present is often edge dependent (i.e. to either light or dark edge only)	When present is not edge dependent (i.e. to both edges).	When present is not edge dependent (i.e. to both edges).
ORIENTATION SPECIFICITY	Sharply tuned	Less sharply tuned than S or B	Sharply tuned
RESPONSE TO RAPIDLY MOVING STIMULI	Usually weak	Usually moderately strong	Usually weak
RESPONSE TO SHORT STIMULI (<0.5° long)	Weak	Strong or weak	Weak

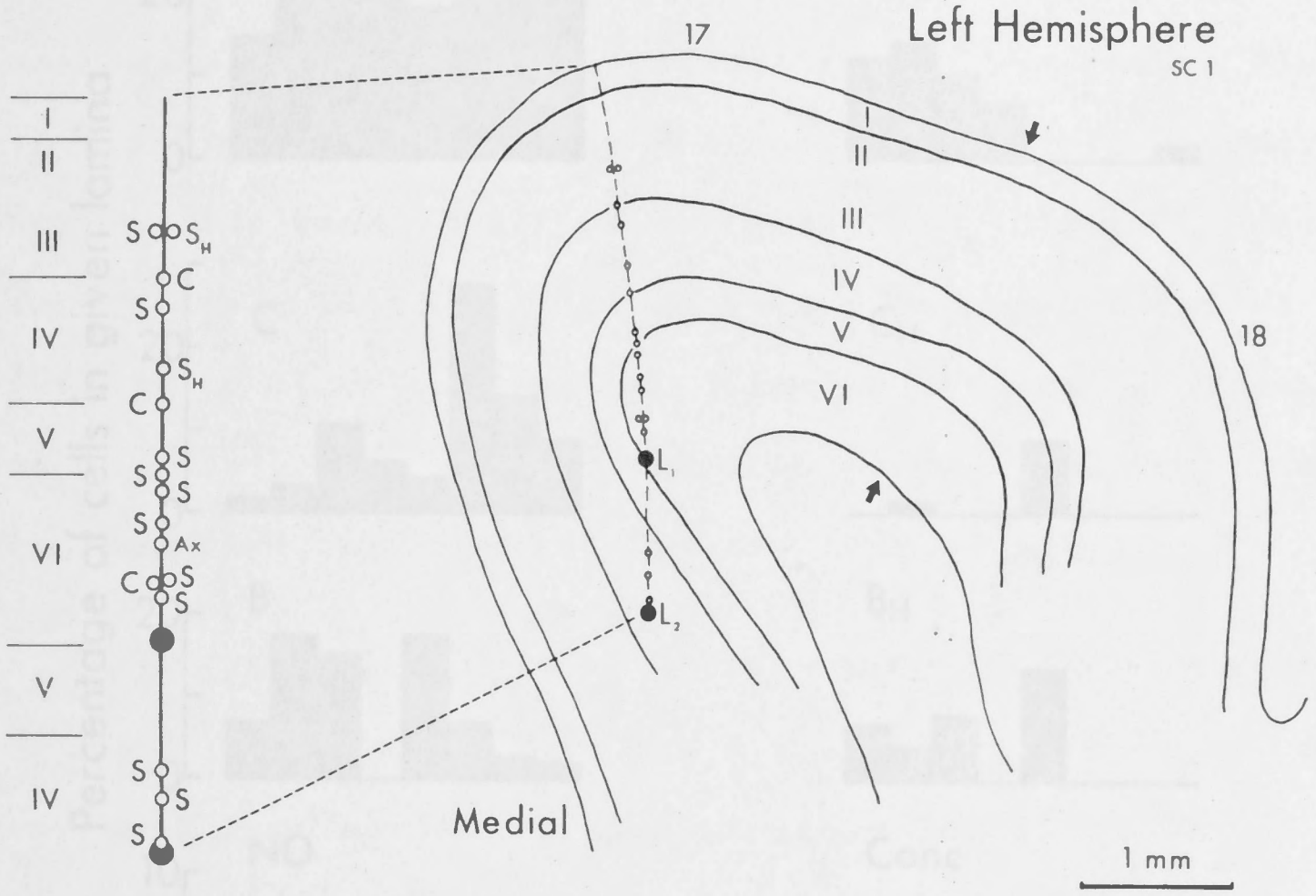


Fig. 4. An electrode penetration in the medial bank of the lateral gyrus (area 17). L, electrolytic lesions; arrows, 17/18 border region; Ax, geniculocortical fibre.

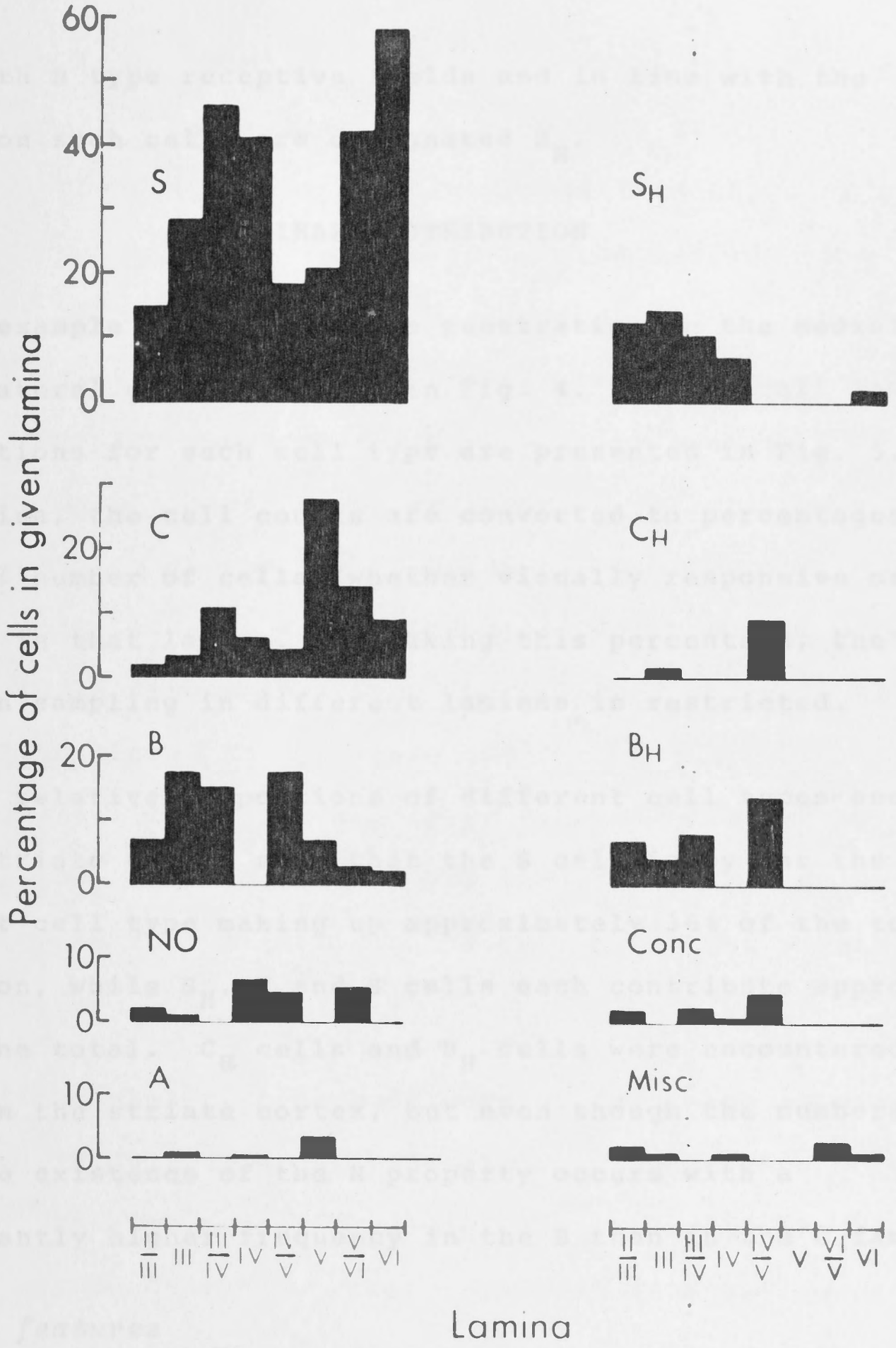


Fig. 5. Laminar distribution of striate receptive field classes. For each cell type, counts are expressed as a percentage of the total number of cells recorded in a given lamina. NO, non-oriented cell; Conc, concentric cell; Misc, cells with mixed receptive field properties.

cells with B type receptive fields and in line with the convention such cells are designated B_H.

LAMINAR DISTRIBUTION

An example of an electrode penetration in the medial bank of the lateral gyrus is shown in Fig. 4. The overall laminar distributions for each cell type are presented in Fig. 5. For each lamina, the cell counts are converted to percentages of the *total* number of cells (whether visually responsive or not) recorded in that lamina. By taking this percentage, the effect of uneven sampling in different laminae is restricted.

The relative proportions of different cell types encountered in the striate cortex show that the S cell is by far the commonest cell type making up approximately 36% of the total population, while S_H, C and B cells each contribute approximately 10% to the total. C_H cells and B_H cells were encountered only rarely in the striate cortex, but even though the numbers are small the existence of the H property occurs with a significantly higher frequency in the B than in the C family.

Specific features

(i) The S cell

As mentioned earlier, the S cell has similar properties to the simple cell of Hubel and Wiesel (1962) and in terms of the heirarchical sequence of information processing would be considered as the first order neuron in the striate cortex. It might be expected, therefore, that cells with S type receptive fields would be concentrated in the laminae which receive

projections from the dLGN. Fig. 5 shows that the highest proportions of S cells are found in laminae IV and VI - a bimodality that becomes even more apparent if cells in the regions bordering these two laminae are merged into the count (i.e. V/VI into VI and IV/V plus III/IV into IV). The border zones between the major laminae (taken as being about 100μ wide) have been separated out in the distribution because 50μ was thought to be the order of error incurred in locating the precise position of the electrode tip in the histologically identified lesion. As a result, cells 50μ on either side of a border could have been placed in the wrong lamina. In reality, therefore, the peaks in the S cell distribution may be even sharper than they appear in Fig. 5. However, S cells are encountered outside laminae IV and VI and Fig. 5 indicates that they make up a significant proportion of the population of every layer.

Since quantitative methods were not employed in assessing receptive fields, it is not possible to state with complete assurance that the receptive fields of the S cells in laminae IV and VI were identical. However, apart from the ocular dominance distributions (see below), there were no obvious points of difference in the S type receptive fields of cells recorded in the two regions.

(ii) The S_H cell

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. As shown in Fig. 5, S_H cells are found most

commonly in the superficial layers of the striate cortex. A significant proportion of units in the upper layers of the striate cortex were unresponsive to visual stimuli. This apparent lack of responsiveness could arise either from damage caused by the recording electrode or from a failure to meet highly selective stimulus requirements for the cell. (cf. Chapter 2, Chapter 3). With regard to the latter possibility, it is perhaps significant that S_H cells were usually the most difficult to define visually. Since S_H cells are confined to the upper laminae it is possible that their presence in the upper part of lamina III and lamina II may account, in part, for the high proportion of unclassed units in these layers. If so, the concentration of S_H cells in the upper reaches of the striate cortex would be more marked than indicated in Fig. 5.

Some S_H cells are encountered in the thalamic receiving layer (lamina IV), but once again, at the qualitative level, significant differences in the receptive field properties of S_H cells in laminae III and IV were not detected.

(iii) The C cell

The laminar distribution of C cells also shows a tendency towards bimodality with peaks centred on lamina V and the III/IV border. The peak at the III/IV border is extremely small but there is no doubt that it rises above the general background level for C cells. By far the highest proportion of C cells is in lamina V while the most marked reduction in concentration occurs in laminae II and III. About 25% of the C cells resembled the complex cell described by Palmer and Rosenquist (1974) in that the cell responded equally well to

small spots or long edges. These neurons were most commonly encountered in the deeper layers. Many C cells however, required summation along the length of the receptive field in order to produce an optimal response. Such cells, in contrast to the Palmer and Rosenquist type cells, were distributed more evenly throughout the striate cortex.

Evidence is presented in Chapter 3 which shows that a number of C units located in laminae IV and VI are efferent to the superior colliculus. Since the cells of origin of cortico-tectal neurons are restricted to lamina V (cf. Chapter 3), it would seem that the recording electrode sometimes records electrical activity from parts of the neuron distal to the cell body. It is possible, therefore, that the proportions of C cells in laminae III, IV and VI (Fig. 5) are an overestimate and that the number of C cells in layer V is, in reality, higher than shown here.

(iv) The C_H cell

The C_H cell was encountered only rarely in the present sample. Kato, Bishop and Orban (1978), using quantitative techniques found a higher proportion of this cell type and from their results it would seem that many of the Palmer and Rosenquist type C cells do in fact possess end-zone inhibitory areas beyond the excitatory discharge regions. All of these cells show very rapid length summation and the optimal stimulus length can be as little as 0.3^{o}. It is possible, therefore, that some of the Palmer and Rosenquist type C cells in the deeper layers, described in the present analysis, may have been C_H cells, end-zone inhibition possibly escaping recognition

because non-optimal stimuli were used. However, there is no doubt that C cells with total end-zone inhibition are extremely rare in the striate cortex.

(v) The B cell

The B cell family (B and B_H) has a clearly defined bimodality in its laminar distribution with no cells of this type being found in lamina IV. The two peaks, which show a similar degree of concentration, are centred in lamina III and on the IV/V border probably in lamina VA. Once again, at the qualitative level, the B cells found at these two sites had substantially similar receptive field properties. One difference in the efferent properties of B cells in lamina III and lamina IV/V is that the more superficial B cells project to the Clare-Bishop cortex (Chapter 4).

(vi) The B_H cell

As implied above, the B_H cell has almost the same laminar distribution as the B cell. There may be a slight difference in the laminar distributions of the two cell types in that B_H cells occur as a higher proportion of the cells in the upper portions of layer III then in lower lamina III, the reverse being true for the B cell. Thus like the S family of cells, the H property occurs more commonly in B cells located in the most superficial cortical layers.

(vii) The non-oriented (N.O.) cell

The non-oriented cell showed no marked preference to stimuli of any particular orientation. Such cells gave mixed

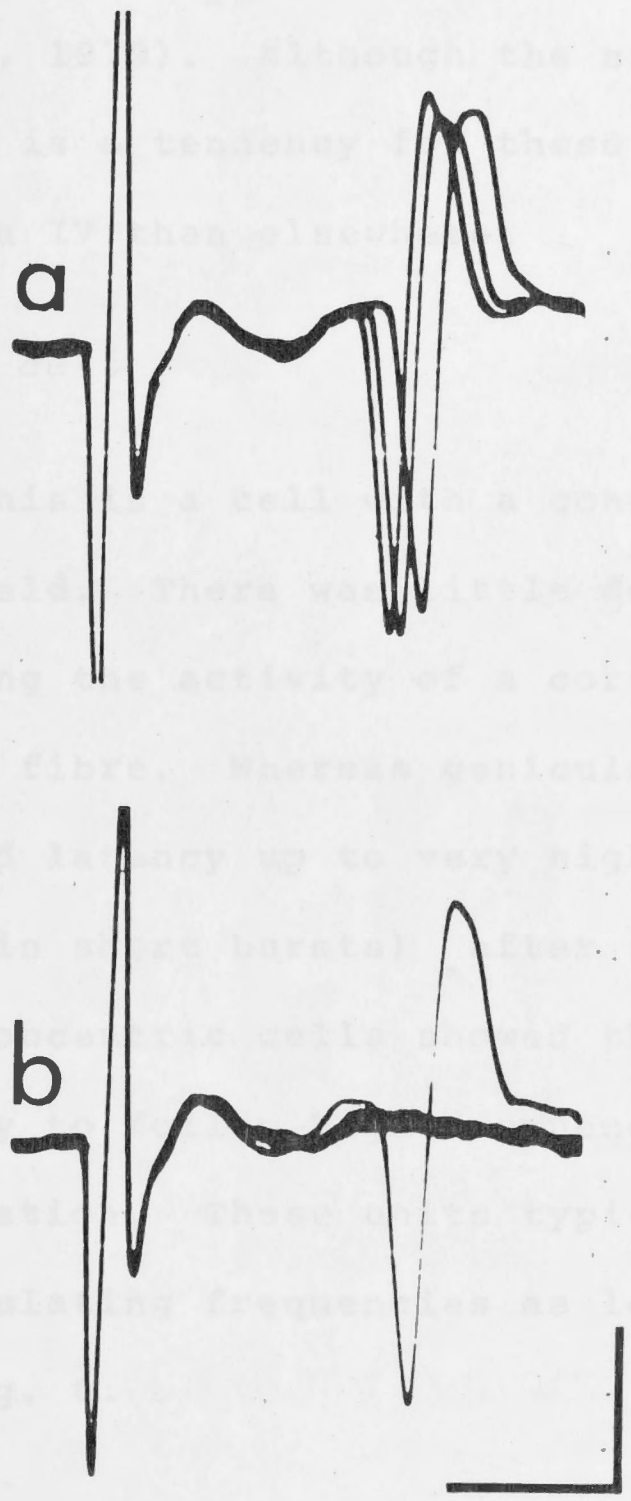


Fig. 6. Orthodromic activation of a striate neuron with a concentrically organized receptive field, produced by electrical stimulation of the optic radiation. a, 1 Hz; b, 10 Hz. Note the latency variation and failure to follow repetitive stimulation. Marker indicates 1 msec and 1 mV.

ON/OFF discharges when tested with stationary flashing lights (cf. Joshua and Bishop, 1970). Although the numbers of such units are small, there is a tendency for these cells to occur more commonly in lamina IV than elsewhere.

(viii) The concentric cell

More precisely, this is a cell with a concentrically organized receptive field. There was little doubt that the electrode was monitoring the activity of a cortical cell and not simply an afferent fibre. Whereas geniculate axons fired repetitively at a fixed latency up to very high stimulus frequencies (1,000 Hz in short bursts) after stimulation of the optic radiation, concentric cells showed the latency variation and inability to follow high frequencies characteristic of transsynaptic excitation. These units typically started to miss responses at stimulating frequencies as low as 10Hz. An example is shown in Fig. 6.

As with the non-oriented cell, the number of recorded cells with concentrically organized receptive fields is too small to allow worthwhile conclusions to be drawn about their laminar distribution, although cells of this kind may also be concentrated in lamina IV. Reliably identified concentric cells have not previously been reported in the cat striate cortex. In the absence of information about the unit's response to optic radiation stimulation it is likely that many of these cells would be regarded as afferent fibres from the dLGN.

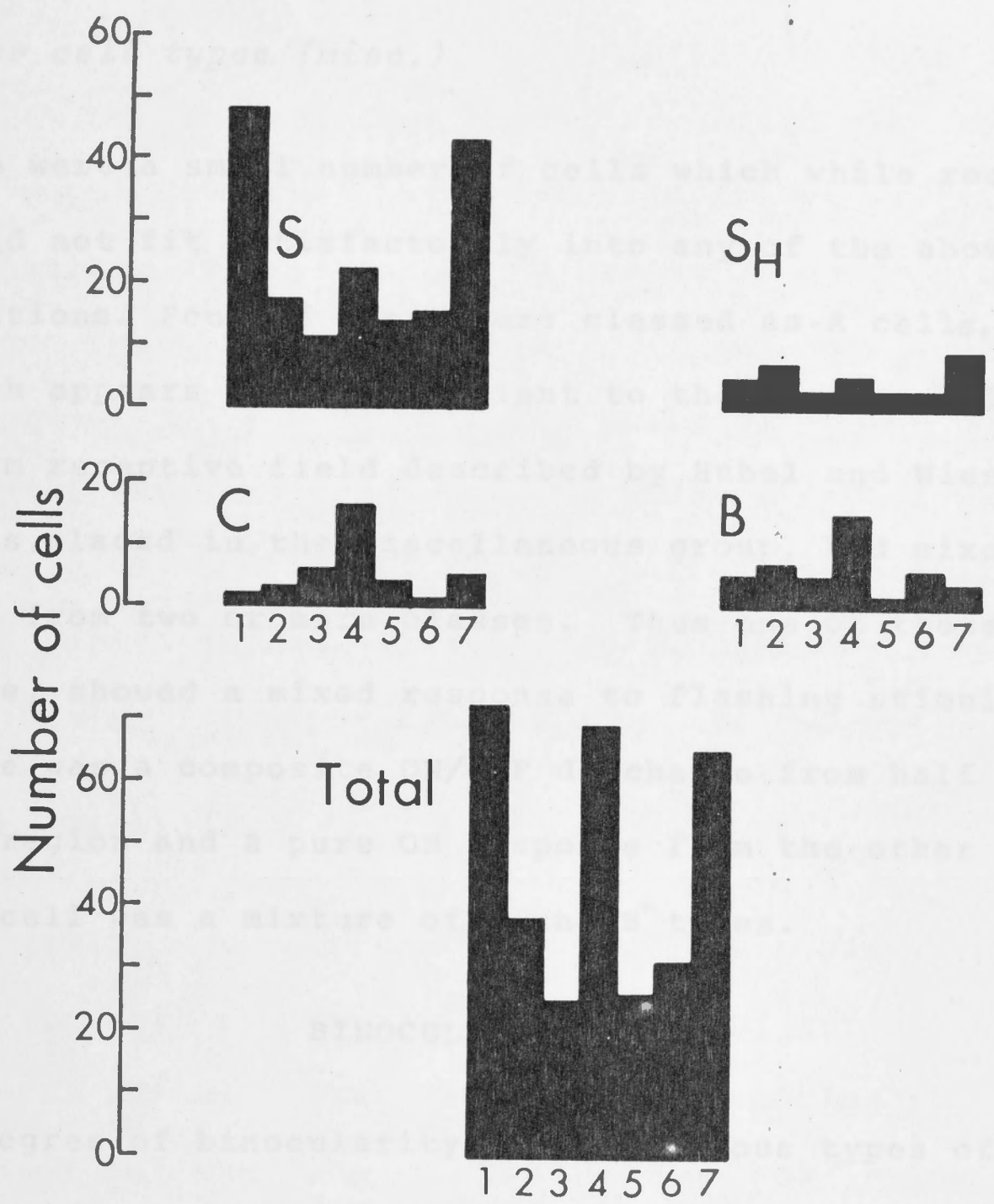


Fig. 7. Ocular dominance distributions for the four most common types of striate neuron and the overall distribution for all cells in area 17. Ocular dominance expressed on a scale ranging from 1 (driven solely by the contralateral eye) to 7 (driven purely by the ipsilateral eye) (Hubel and Wiesel, 1962).

(ix) Other cell types (misc.)

There were a small number of cells which while responsive enough, did not fit satisfactorily into any of the above classifications. Four of these were classed as A cells, a group which appears to be equivalent to the complex cell with non-uniform receptive field described by Hubel and Wiesel (1962). Five others, placed in the miscellaneous group, had mixed properties from two or more classes. Thus one of these cells, for example, showed a mixed response to flashing stimuli in which there was a composite ON/OFF discharge from half the discharge region and a pure ON response from the other half; as if the cell was a mixture of S and B types.

BINOCULARITY

The degree of binocularity of the various types of striate neuron was expressed on a dominance scale ranging from 1 to 7, cells in these two groups being driven purely by the contralateral and ipsilateral eyes respectively (Hubel and Wiesel, 1962). Since the ocular dominance histograms in Fig. 7 record the numbers of a particular cell and are not related to the laminar distribution, the population has been increased by including 173 units of uncertain laminar disposition.

The ocular dominance histogram for the total population (Fig. 7) reveals that a similar number of cells are driven from the ipsilateral eye, the contralateral eye, or with equal effectiveness from either eye. There is a slight bias towards the contralateral eye; cells in ocular dominance groups 1, 2 and 3 make up 43% of the population compared with 37% for cells

in groups 5, 6 and 7. Significant differences are apparent in the distributions of individual receptive field classes. In the S cell population, 56% have monocular receptive fields and there is a marked depression in the number of units driven with equal effectiveness from either eye (i.e. cells in ocular dominance group 4). A more detailed analysis of the ocular dominance distributions of S cells is undertaken below. In contrast, only 15% and 25% of C and B cells respectively are monocularly activated and a high proportion in both groups are activated equally or almost equally from the two eyes.

Effect of eccentricity

Albus (1975) has reported that there is a higher proportion of binocularly activated units in the area of cortex representing the peripheral visual field than that representing the centre (i.e. within 4^{o} of the area centralis). On this point, the present results are somewhat equivocal and give only weak support to Albus's findings. With regard to all cell types, 44% of cells with central receptive fields were monocular (ocular dominance groups 1 and 7) while of the peripheral units 39% were monocular. When considered in terms of receptive field types, 51% of central S cells were monocular compared to 55% in the periphery. For C cells, 28% of the central population were monocular in comparison to 10.5% in the periphery and for B cells, monocular units made up approximately 17% of both the central and peripheral populations. The observation that C cells generally become more binocular in the periphery, while the degree of monocularity of S cells remains fairly constant is in direct contrast to the results of Albus (1975). A reason for this difference may lie

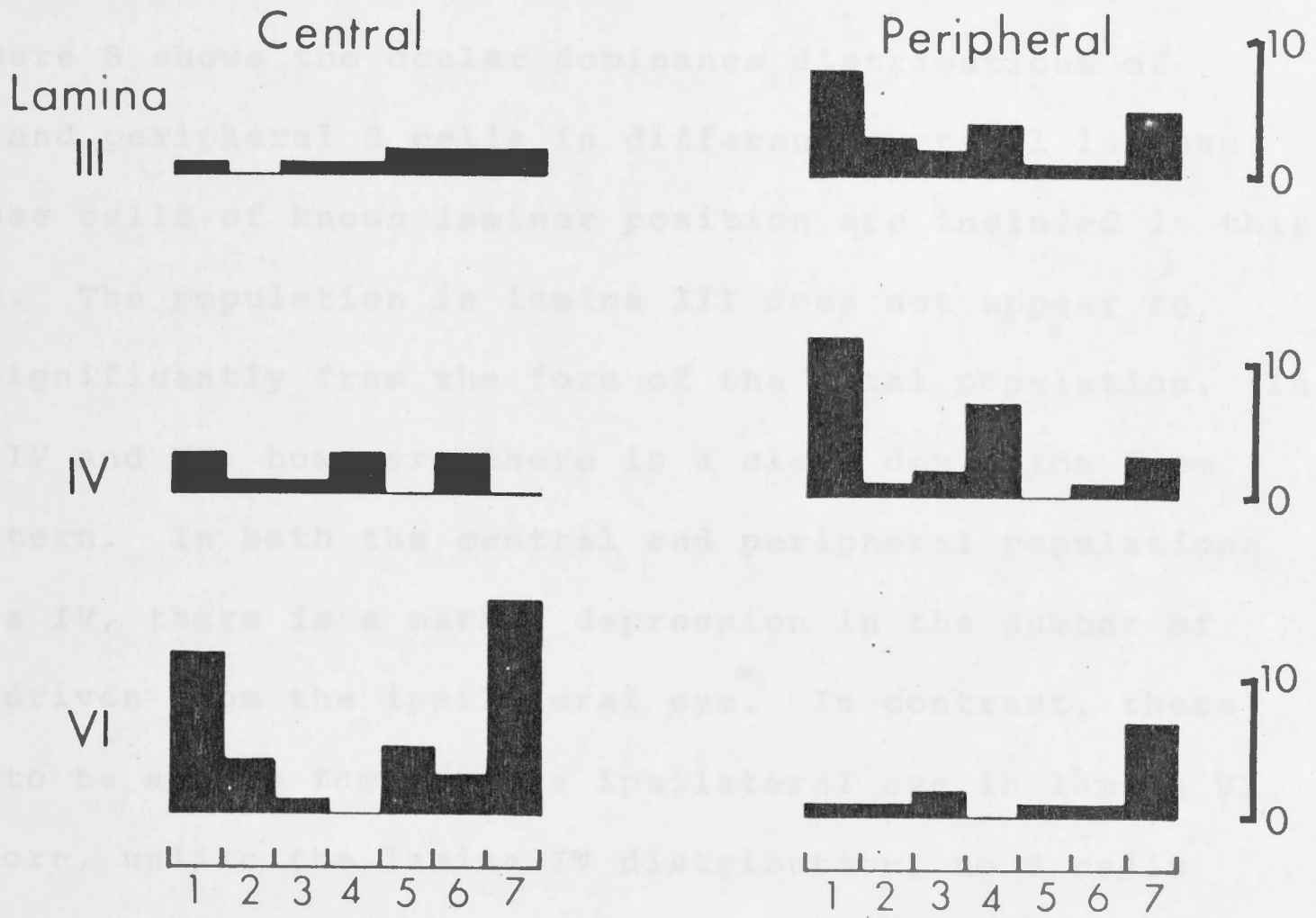


Fig. 8. Ocular dominance distribution of central and peripheral S cells in different cortical laminae of area 17. Central, receptive field centres within 4° of the area centralis; peripheral, receptive field centres greater than 4° from the area centralis.

in the fact that the ocular dominance distribution of S cells varies from layer to layer (see below).

S cells in different laminae

Figure 8 shows the ocular dominance distributions of central and peripheral S cells in different cortical laminae. Only those cells of known laminar position are included in this analysis. The population in lamina III does not appear to differ significantly from the form of the total population. In laminae IV and VI, however, there is a clear deviation from this pattern. In both the central and peripheral populations of lamina IV, there is a marked depression in the number of S cells driven from the ipsilateral eye. In contrast, there appears to be a bias *towards* the ipsilateral eye in lamina VI. Furthermore, unlike the lamina IV distribution, no S cells in lamina VI are found in ocular dominance group 4.

In the interpretation of these statistics it should be stressed that only the excitatory component in the response of the cell has been considered. The activation of inhibitory regions in the receptive field has a very important modulating influence upon the binocular response, particularly in the encoding of disparity information (e.g. Nelson, Kato and Bishop, 1977). Many of the so called monocular units could receive a strong inhibitory input from the non-dominant eye but such regions are not readily recognised using qualitative methods of investigation.

AFFERENT INPUT TO AREA 17

General comments

In 19 cats, stimulating electrodes were positioned in both the optic chiasm (OX) and the optic radiation (OR), whereas in 15 cats they were placed only in the optic radiation. (see METHODS). The following analysis is based on the measurement of the minimum or shortest latency observed for the first spike induced by orthodromic activation. Generally, an orthodromically activated spike had a latency that varied over a range of approximately 0.3 to 0.5 msec and the minimum latency (hereafter referred to simply as the latency) provided a consistent measure largely independent of variations in transmission delay.

Cells excited from OR

Only cells for which the laminar position was unambiguously determined are included in this analysis. In total, 431 units were tested with OR stimulation of which 173 (40%) could be orthodromically excited. The population of electrically excitable cells includes those driven by electrical stimulation alone as well as those which fired only when the conditioning technique was used (see METHODS). Table 2 shows the number and proportion of each striate cell type that were orthodromically activated by optic radiation stimulation. All of the non-oriented and concentric units were activated. Interestingly, cells in the B and C families (i.e. B and B_H, C and C_H) were more commonly excited than S or S_H cells.

Latencies to OR stimulation

The orthodromic OR latencies of the 173 striate neurons are

TABLE 2

Striate cell responses to electrical stimulation of the optic radiation

	RECEPTIVE FIELD TYPE									
	S	S_H	C	C_H	B	B_H	N.O.	Conc	Misc	NVC
DRIVEN	59	13	18	3	19	4	9	4	1	43
NOT DRIVEN	100	20	15	1	15	6	0	0	6	95
% DRIVEN	37.1	39.4	54.5	75.0	55.9	40.0	100.0	100.0	14.3	31.2

N.O.: Non-oriented

Conc: Concentric

Misc: Other cell types

NVC : Not visually classified

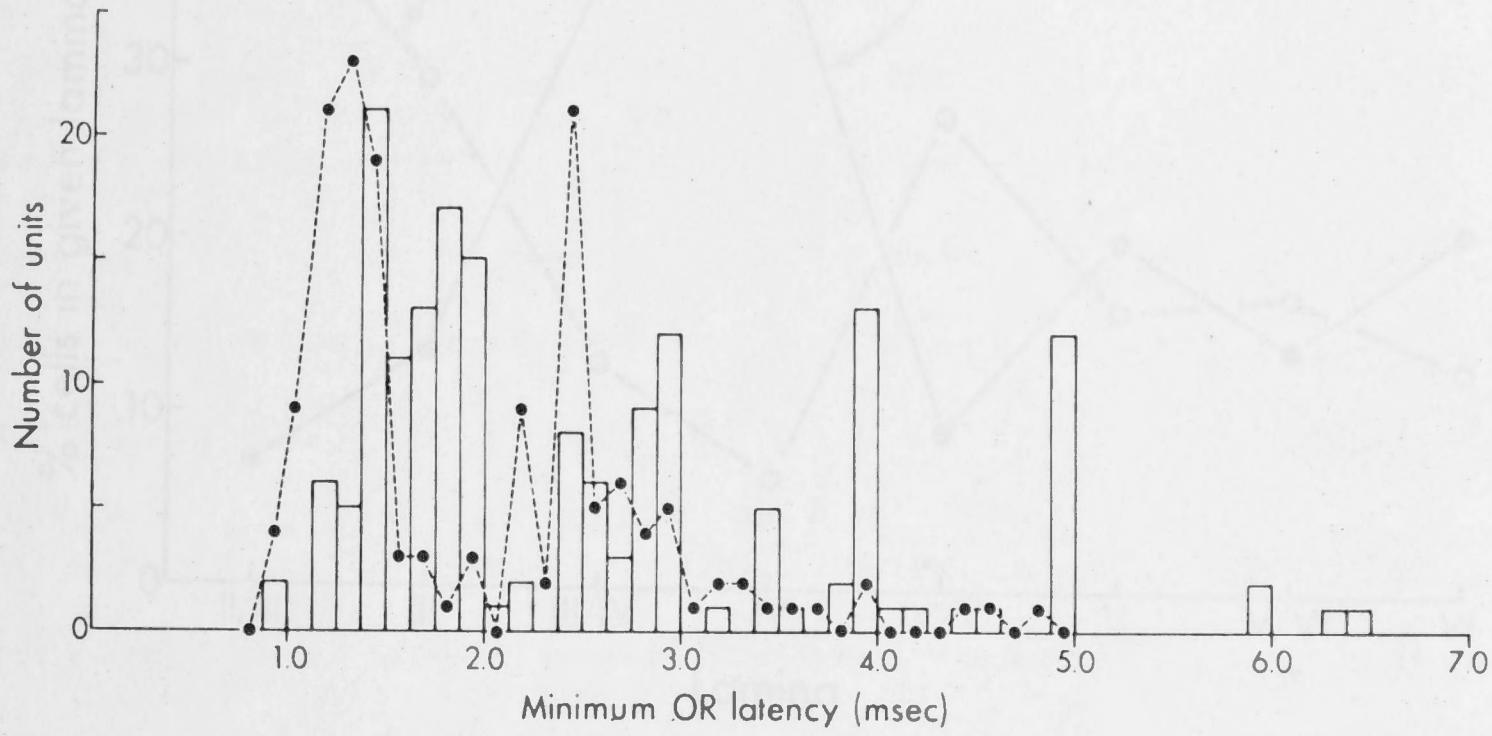


Fig. 9. Minimum orthodromic optic radiation latencies of striate neurons (open blocks). The filled circles joined by the dashed line indicate the optic radiation latencies of cells in area 18.

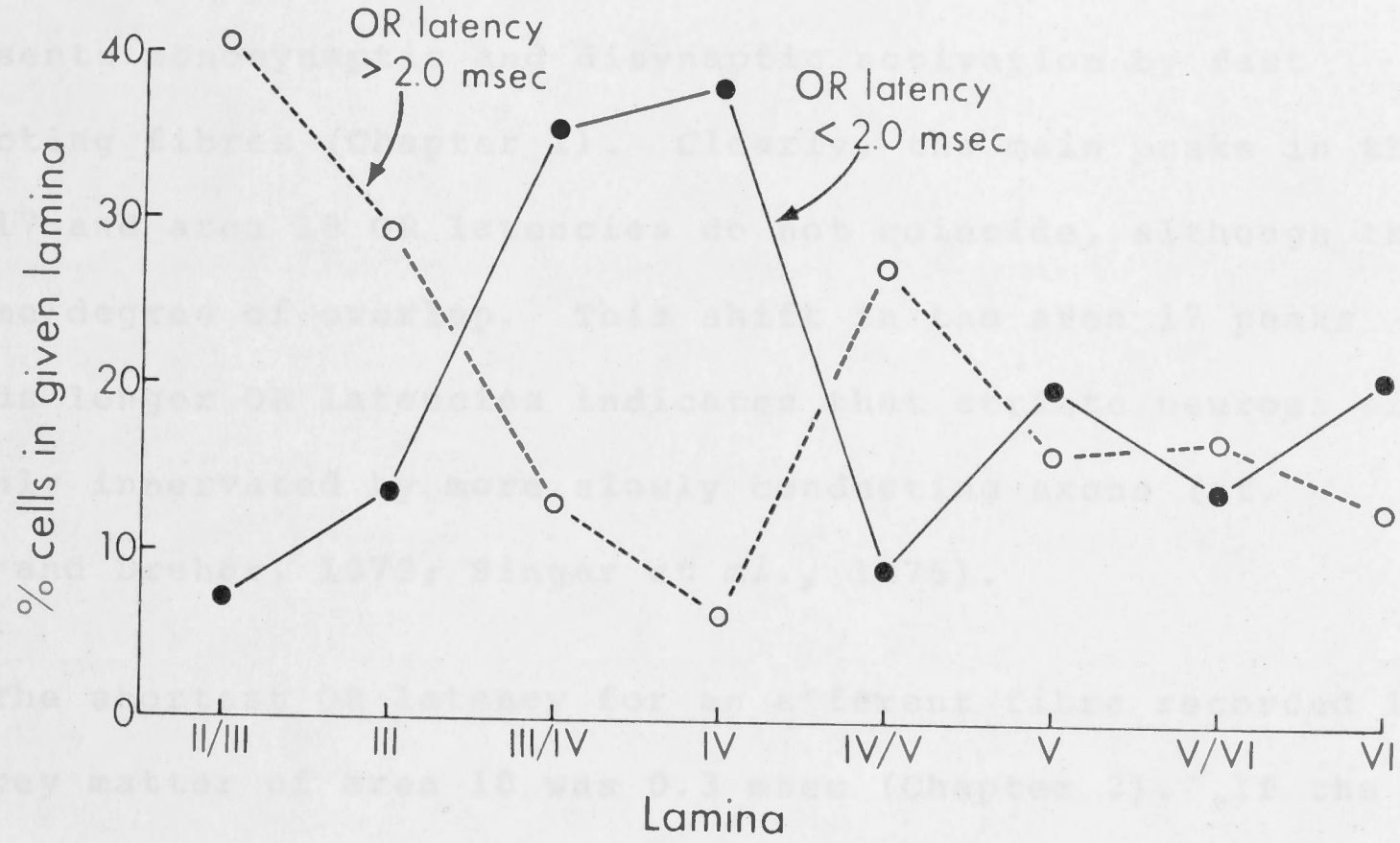


Fig. 10. Laminar distribution of striate cells with minimum orthodromic optic radiation latencies less than or greater than 2.0 msec. Proportion of each latency group is expressed as a percentage of the total number of cells encountered in a given lamina.

presented in Fig. 9. These data are plotted as the rectangular columns and for comparison, the OR latencies for parastriate neurons are also shown as the filled circles and continuous line (cf. Chapter 2). The bimodality of the area 18 OR latencies represents monosynaptic and disynaptic activation by fast conducting fibres (Chapter 2). Clearly, the main peaks in the area 17 and area 18 OR latencies do not coincide, although there is some degree of overlap. This shift in the area 17 peaks towards longer OR latencies indicates that striate neurons are commonly innervated by more slowly conducting axons (cf. Stone and Dreher, 1973; Singer *et al.*, 1975).

The shortest OR latency for an afferent fibre recorded in the grey matter of area 18 was 0.3 msec (Chapter 2). If the transmission delay is 0.8 msec (cf. Chapter 2), the earliest possible disynaptic response (assuming a small additional delay for conduction of the impulse between the two cortical cells) will be 2.0 msec. Hence all striate neurons with OR latencies less than 2.0 msec can be considered as being monosynaptically excited by afferent fibres. It is likely that a number of striate cells with latencies longer than 2.0 msec are also directly excited, but on the basis of OR latencies alone it is not possible to differentiate between slow direct and fast indirect innervation (cf. Stone and Dreher, 1973).

Figure 10 shows the laminar distribution of striate cells with OR latencies less than or greater than 2.0 msec. The proportion of each latency group is shown as a percentage of the total number of cells (whether driven or not driven) encountered in a given lamina. Monosynaptically driven cells

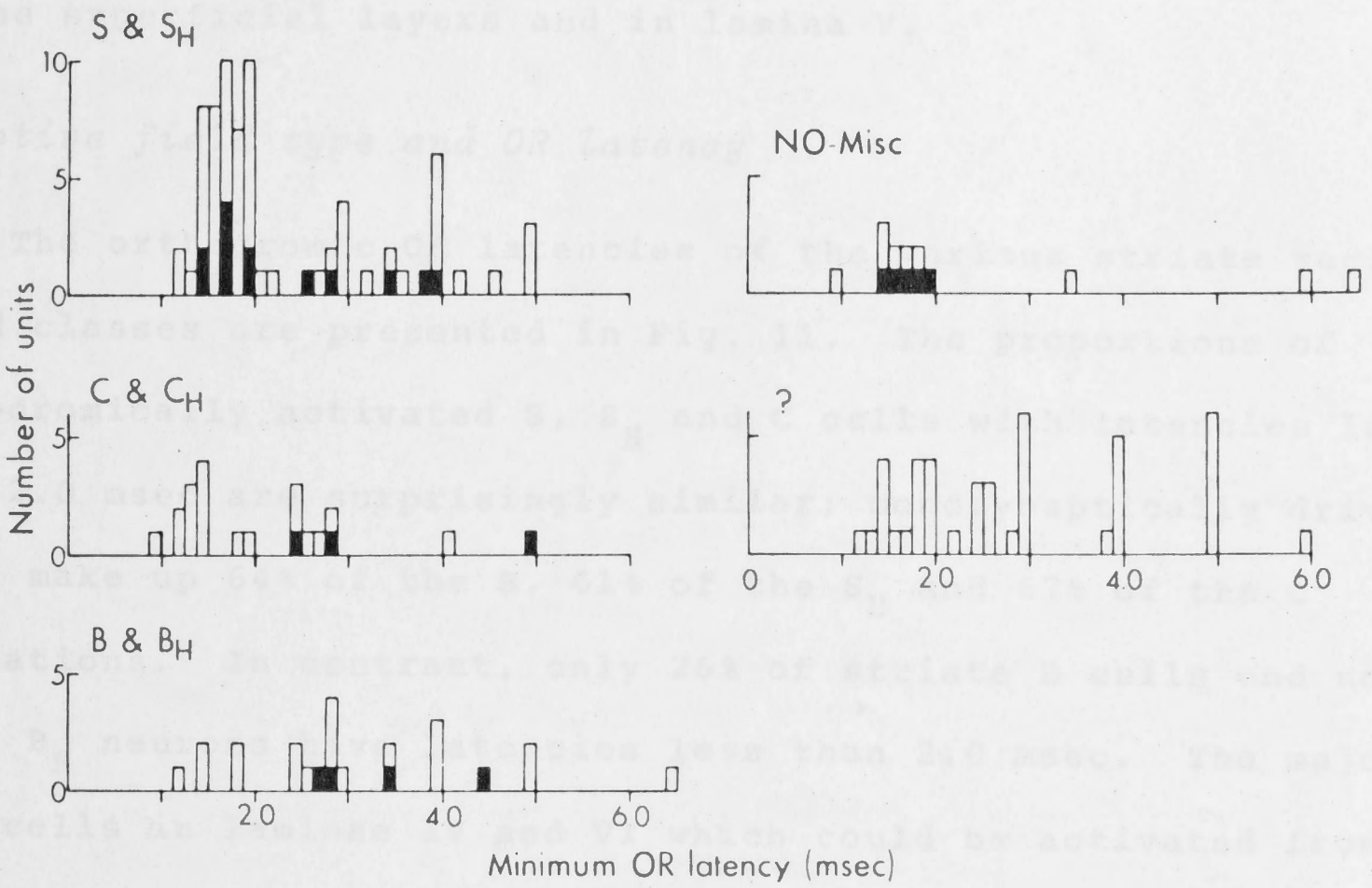


Fig. 11. Minimum orthodromic optic radiation latencies of each striate receptive field class. Open blocks, S, C, B, NO; filled blocks, S_H, C_H, B_H, Misc; ?, unclassified cells.

are most common in laminae IV and VI, the layers shown anatomically to receive geniculocortical afferents. In contrast, cells with OR latencies greater than 2.0 msec are most frequent in the superficial layers and in lamina V.

Receptive field type and OR latency

The orthodromic OR latencies of the various striate receptive field classes are presented in Fig. 11. The proportions of orthodromically activated S, S_H and C cells with latencies less than 2.0 msec are surprisingly similar; monosynaptically driven cells make up 64% of the S, 61% of the S_H and 67% of the C populations. In contrast, only 26% of striate B cells and no C_H or B_H neurons have latencies less than 2.0 msec. The majority of S cells in laminae IV and VI which could be activated from the optic radiation are monosynaptically excited (75% and 72% respectively). This is also true for the smaller C cell population and to a large extent for the non-oriented and unclassified cell groups. In contrast, 86% of B, B_H and C_H cells with OR latencies greater than 2.0 msec are located in laminae II and III. It is interesting to note that S_H cells resemble S cells and B_H cells resemble B cells in their afferent connectivity, wereas C_H cells appear to differ from the rest of the C population. There were no apparent differences in the receptive field properties of S or of C cells with OR latencies less than or greater than 2.0 msec.

Of the cells with orthodromic latencies less than 2.0 msec, C cells generally have latencies less than 1.5 msec whereas the majority of S and S_H cells have latencies that lie between 1.5 and 2.0 msec(Fig.11). This suggests that monosynaptically excited

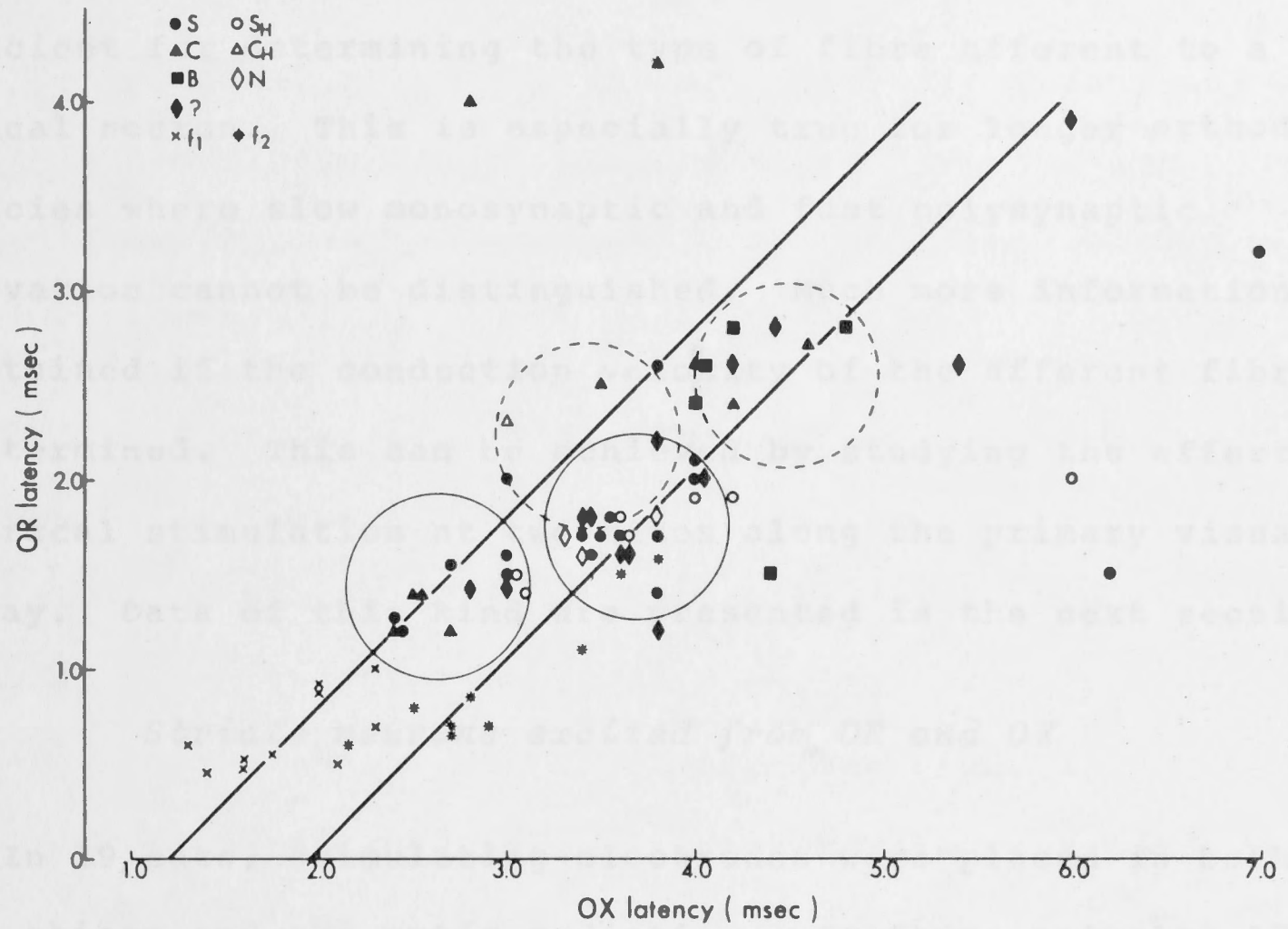


Fig. 12. Orthodromic optic chiasm (OX) and optic radiation (OR) latencies of striate neurons and geniculocortical fibres recorded within area 17. f_1, brisk transient fibres; f_2, brisk sustained fibres. The two lines indicate the mean OX-OR latency difference of f_1 and f_2 groups respectively. For further explanation - see text.

C cells tend to be driven by fast axons, while S and S_H cells are directly innervated by more slowly conducting afferent fibres. In general however, OR stimulation alone is not sufficient for determining the type of fibre afferent to a cortical neuron. This is especially true for longer orthodromic latencies where slow monosynaptic and fast polysynaptic innervation cannot be distinguished. Much more information is obtained if the conduction velocity of the afferent fibre is determined. This can be achieved by studying the effect of electrical stimulation at two sites along the primary visual pathway. Data of this kind are presented in the next section.

Striate neurons excited from OR and OX

In 19 cats, stimulating electrodes were placed in both the optic chiasm and the optic radiation. In these animals, 137 cells were activated from the radiation of which 57 (42%) were also driven from the chiasm. Unlike much of the previous analysis, these populations include cells of uncertain laminar disposition.

Figure 12 presents the OX and OR latencies of the striate cells excited from both sites. Also shown are the OX and OR latencies of 19 geniculocortical fibres recorded within the grey matter of area 17. The OX-OR difference provides a measure of the time taken for the conduction of an impulse from the chiasm, through the dLGN to the optic radiation. With one exception, it was found that afferent fibres with an OX-OR difference of 1.6 msec or less had receptive field properties typical of a brisk transient (Y) type, while all fibres with an OX-OR

difference greater than 1.6 msec had receptive fields of the brisk sustained (X) type. This latency distinction is very similar to that described for Y and X cells by Hoffmann, Stone and Sherman (1972). For convenience, the brisk transient and brisk sustained populations will be termed group 1 and group 2 respectively and the two groups are shown by the crosses and asterisks in Fig. 12.

The mean OX-OR latency differences of group 1 (crosses) and group 2 (asterisks) fibres are 1.20 and 1.95 msec respectively. The solid lines in Fig. 12 pass through all points at which the OX latency is equal to the OR latency plus 1.20 msec (for group 1) and 1.95 msec (for group 2). The intercept of these lines with the abscissa indicates the mean OX-OR difference for the two groups. Clearly, if striate cortical neurons are innervated by fibres from one or other of the afferent groups, the OX-OR latency differences of these cortical cells will have mean values of either 1.20 or 1.95 msec. As a result, the plotted points of the striate neurons (whatever their absolute OX and OR latencies) should lie close to one or other of the two lines shown in Fig. 12. An examination of Fig. 12 reveals that, in general, striate cells do indeed lie close to one or other of these two lines but the degree of scatter makes it difficult to assess with any certainty the type of fibre afferent to these neurons.

The situation is clarified when the OX and OR latencies of group 1 and group 2 fibres are considered. The mean OX and OR latencies of group 1 fibres is 1.83 and 0.63 msec and for group 2 fibres is 2.9 and 0.95 msec respectively. Assuming the

transmission delay across a synapse is 0.8 msec (Chapter 2), then populations of striate neurons monosynatpically excited by either group 1 or group 2 fibres would have mean OX and mean OR latencies of 2.63 and 1.43, and 3.7 and 1.75 msec respectively. The two continuous circles in Fig. 12 have been centred on these points. To allow for population scatter, the reference circles have been drawn with a radius equivalent to 0.5 msec - selected because such a circle encompasses most of the scattered points (crosses) for group 1 axons. A greater scatter is present in the points (asterisks) representing the group 2 fibres and accordingly the points representing cortical cells monosynaptically activated by this group have a greater chance of falling outside the corresponding circle. Nonetheless, the two circles give a good indication of where the plotted points would fall for cells driven directly by the two groups of axons. The two dotted reference circles in Fig. 12 are centred at OX and OR latencies of 3.43 and 2.23, and 4.5 and 2.55 msec respectively. These circles have been drawn to provide an indication of where disynaptically activated cells would occur.

As mentioned earlier, only about 40% of the striate cells activated from OR were also excited from the OX stimulating electrodes. Despite the smaller sample, the OX-OR comparison shown in Fig. 12 allows the number of synaptic delays to be assessed with greater certainty and increases the confidence with which cells are assigned an ordinal position in the cortex. Furthermore, it is possible to comment on the type of fibre afferent to striate neurons. Cells with the S type of receptive field make up half of the classified cells (14/28)found in the

two monosynaptic reference circles in Fig. 12. Similar proportions of S cells are found in each of the two reference circles suggesting that individual S cells may be driven monosynaptically by either group 1 or group 2 geniculocortical axons (cf. Singer *et al.*, 1975). Four S cells are found outside the limits of the monosynaptic reference circles. The OX-OR latencies of two of these cells are suggestive of innervation by axons conducting even slower than the group 2 fibres. The other two S cells may be disynaptically driven by group 1 axons. With regard to the laminar distribution, the location of 9 of the 14 S cells falling in the monosynaptic reference circles was unambiguously determined. Of these 9, 5 were found in lamina IV or at the III/IV border and 2 were located in lamina VI.

The location of data points representing most S_H cells is also consistent with a monosynaptic drive from either group 1 or group 2 axons. Some C cells also appear to be monosynaptically activated and it should be stressed that the 4 examples of this type all fall in the monosynaptic reference circle associated with group 1 fibres. A few C cells have OX and OR latencies indicative of disynaptic activation by either group 1 or group 2 fibres. Of the other cell types, the B type are not found within either monosynaptic reference circle but are often activated indirectly by thalamic afferents. All non-oriented cells occur in the reference circle of the group 2 geniculocortical axons.

DISCUSSION

The laminar distribution of striate receptive field classes: a comparison with previous studies

A number of previous studies have examined the laminar distribution of receptive field classes in the striate cortex (Hubel and Wiesel, 1962; Kelly and Van Essen, 1974; Gilbert, 1977; Sillito, 1977a; Kato, Bishop and Orban, 1978). The present data indicate that S cells are the most commonly occurring cell type in area 17 and are concentrated in lamina IV and lamina VI. These results are therefore in agreement with those of Hubel and Wiesel (1962) and Kato *et al.* (1978). The high proportion of S cells in lamina IV has also been observed by Kelly and Van Essen (1974), Gilbert (1977) and Sillito (1977a). However both Kelly and Van Essen (1974) and Gilbert (1977) have reported that complex (or C) cells predominate in lamina VI. In this context, a comparison with Sillito's work cannot be made since he did not record from layer VI.

In laminar VI, Gilbert (1977) found three times as many standard complex as simple cells. By contrast, S cells made up the bulk of the classified cells (81%) in lamina VI in the present sample and B and C cells only contributed 14% to the total of classified cells. Gilbert's criteria for identifying simple cells are not identical to those used in the present study with the result that many S cells would almost certainly be classed as standard complex cells by Gilbert (1977). The major difference in the two classifying schemes appears to be that those cells which have either a weak response to flashing stimuli or a single ON or OFF discharge region in their receptive

field have been placed in the standard complex category by Gilbert (1977), while I have classed them as S cells. The warrant for taking this step is that in all other properties these cells resemble S cells. Moreover, areas of weak flashing light discharge will often produce a consistent response with intensive testing. Finally, in principle, it is better to avoid classifying a cell on the basis that its response to a stimulus (in this case flashing bars) is weak or absent.

It would seem therefore, that the distinction between the lamina VI populations of this and Gilbert's study is at least partly related to a divergence in the criteria used for the classification of striate receptive fields. Such a proposal has also been put forward by Kato *et al.* (1978). However, as described in Chapter 3 (cf. Harvey, 1978), there still appears to be an inconsistency with regard to the conduction velocity of the axons of lamina VI cells projecting to the dLGN. Slow conducting corticogeniculate S cells were not reported by Gilbert (1977) although they constitute the majority in the experiments reported in Chapter 3. As argued in Chapter 3 this discrepancy suggests that, as well as differences in receptive field classification, there may also be differences in the cell populations sampled by the different electrodes used in the two studies.

The laminar distribution of Kelly and Van Essen (1974) contains only cells stained intracellularly and cells whose positions were marked by cell fragments or by extracellular dye. Since such an analysis is almost certainly biased towards the larger neurons and since S cells in lamina VI are likely to have

small somata (Chapter 3, Harvey, 1978), the discrepancy between their results and those described in the present study may again result from a difference in sampling bias.

From intracellular staining with procion yellow, it appears that the majority of simple or S cells in lamina IV are spiny stellate neurons (Kelly and Van Essen, 1974). Golgi studies indicate that spiny stellate neurons do not occur outside lamina IV (Lund, Henry, Macqueen and Harvey, in preparation) and the S cells of lamina VI, many of which send axons to the dLGN, are almost certainly pyramidal neurons. In consequence, the spiny stellate neuron of lamina IV and the pyramidal neuron of lamina VI appear to generate similar, if not identical, response patterns. The receptive fields of S cells in laminae IV and VI were not studied quantitatively, but at the qualitative level the response properties of S cells in the two layers closely resemble one another. There is, however, a difference in the ocular dominance distributions of lamina IV and lamina VI S cells (Fig. 8). The reason for this distinction is not clear but it may be related in some way to the fact that lamina VI S cells project back to the dLGN (Chapter 3). Gilbert (1977) found the length of receptive fields (separation of lateral borders) to be much greater in layer VI than in layer IV simple cells. In the present study, the receptive fields were plotted as minimum response fields and a difference of this kind was not observed. Presumably such differences in the length of the receptive fields may not be observed unless the lengths are determined from length-response curves (cf. Kato *et al.*, 1978).

There is a growing belief that the class of complex cells originally described by Hubel and Wiesel (1962) as having a uniform receptive field can be divided into subclasses. Within this group of cells (which give a composite ON/OFF discharge to flashing stimuli), two types have been identified in the present study. B cells generally have small receptive fields, no or only low spontaneous activity, are sharply tuned for stimulus orientation and commonly prefer slower stimulus velocities. In contrast, C cells have larger receptive fields, have a comparatively high spontaneous discharge, are broadly tuned for orientation and often respond to fast as well as slow stimulus speeds. These two types of cell have a very specific laminar distribution - the C cell being concentrated in lamina V and the B cell in laminae II and III and at the IV/V border (Fig. 5).

Within the C cell population there may also be two subtypes in that some cells show very rapid summation along the length of the receptive field while others produce a maximal response only when long edges are used. The first type resemble the cells described by Palmer and Rosenquist (1974) and are commonly encountered in the deeper layers. As described in Chapter 3, these cells exhibit a high degree of direction selectivity. The second type of C cell is distributed more evenly through the cortex and often shows only weak directional specificity.

Support for the B and C cell subdivision comes from the observation that the subclasses projecting to a given efferent site conform closely to type. Thus C cells in lamina V (including both of the types described above) project to the

superior colliculus and certain thalamic nuclei (Chapter 3) whereas B cells in lamina III are efferent to the Clare-Bishop cortex (Chapter 4). The B cell seems identical with the complex cells in laminae II and III described by Camarda and Rissolatti (1976a). B cells are commonly encountered in the superficial layers but also occur at the border between laminae IV and V. It is not known whether a similar distribution holds for the complex cells described by Camarda and Rizzolatti (1976a) since their report was restricted to an analysis of laminae II and III.

Basing his classification on the influence of iontophoretically applied bicuculline, Sillito (1977a) has proposed that there are three subclasses of complex cell with a uniform receptive field (i.e. not divisible into separate areas of ON or OFF discharge). The type I cell has a low spontaneous activity, a small receptive field and is sharply tuned for stimulus orientation. Directional specificity in these cells is eliminated during the iontophoretic application of bicuculline and cells of this type are commonly located in lamina III. The type I complex cell of Sillito therefore closely resembles the B cell described in the present study. Again however, a concentration of type I cells at the IV/V border is not described by Sillito (1977a). The type II and type III complex cells would probably be included in the C category. Both types have a relatively high spontaneous activity and have large receptive fields. Type II cells commonly show little direction selectivity and any specificity is unaffected by the application of bicuculline. According to Sillito (1977a), type III complex

cells resemble the complex cells described by Palmer and Rosenquist (1974). They are commonly direction selective and direction specificity is not eliminated by bicuculline. However the cells exhibit a powerful suppression of the resting discharge when the stimulus is moved in the non-preferred direction. An exact analogy with the Palmer and Rosenquist type complex cell breaks down since not all of Sillito's type III cells exhibit rapid spatial summation along the length of the receptive field.

With regard to the laminar distribution, type II complex cells are found in both laminae III and V whereas type III cells are concentrated almost entirely in lamina V (Sillito, 1977a). Type II cells are similar to the C cells which respond optimally to elongated stimuli and which show little direction selectivity. It is significant therefore that these C cells are distributed throughout the cortex and commonly occur in lamina III and lamina V. The type III cells of Sillito (1977a) on the other hand, resemble the C cells which show little or no length summation. Both of these types are prevalent in the deeper layers, especially in lamina V.

Gilbert (1977) has also subdivided the complex group into two types. His standard complex cell prefers longer stimuli, has low spontaneous activity, prefers slower velocities and is sharply tuned for stimulus orientation. The special complex cell is in every respect similar to the cell described by Palmer and Rosenquist (1974). In agreement with the present results and those of Sillito (1977a) special complex cells are most frequent in layer V although others are found in lamina III.

The standard complex cell is distributed throughout laminae II, III, V and VI. At first sight, the receptive field properties of Gilbert's standard complex cell resemble those of the B cells described in this study and the type I complex cell of Sillito (1977a). However, as pointed out earlier, some of the standard complex cells have in fact been classified as S in the present study. This may explain the presence of many of these cells in lamina VI of Gilbert's study. In addition, his standard complex group must also include the C cells which prefer longer edges and the type II complex cells of Sillito (1977a).

In agreement with previous reports (Kelly and Van Essen, 1974; Camarda and Rizzolatti, 1976a; Sillito, 1977a,b; Kato *et al.*, 1978) hypercomplex cells are found most commonly in the superficial layers of the striate cortex (Fig. 5). However there is also a tendency for C_H and B_H cells to occur at the top of lamina V. Kato *et al.* (1978) have also shown that hypercomplex II (C_H) cells are concentrated in this layer. The complex cells of Kato *et al.* (1978) all respond optimally to stimuli longer than 2^o, while hypercomplex II cells show very rapid spatial summation and then marked inhibition as the stimulus continues to be lengthened. Both of these cells would have been placed in the C family as defined in the present study. It would appear that the hypercomplex II group resembles the Palmer and Rosenquist type C cell (type III of Sillito (1977a), special complex of Gilbert (1977)) and it is therefore significant that these cells are commonly found in lamina V.

In general, there is reasonable agreement between the present laminar distribution of striate cell classes and those of earlier studies. The differences described above are likely

to be related both to differences in the criteria employed for receptive field classification and perhaps to the sampling of different populations of cortical neurons. The overall picture that emerges is that S or simple cells are concentrated in the layers which receive thalamic afferents while the various subclasses of C or complex cell are more commonly encountered in non-receiving laminae. There are clearly some differences in the way the complex group is subdivided and although a general pattern is emerging, more information is required before the exact nature of the subdivisions can be resolved.

The afferent input to area 17

In the present study, only 40% of striate neurons could be activated by OR stimulation. Of these about 40% were also driven from the optic chiasm. By contrast, 71% of all parastriate neurons were excited from the optic radiation of which 75% were also activated from the OX stimulating electrodes (Chapter 2). Clearly then, cells in the striate cortex are much harder to drive than cells in area 18. This distinction has also been reported by Stone and Dreher (1973) and Singer *et al.* (1975)

As shown in Fig. 9, the minimum OR latencies of cells in area 17 are in general longer than those of parastriate neurons. Consistent with this, no cells in area 18 (cf. Fig. 10, Chapter 2) are represented by the plotted points that fall within the monosynaptic reference circle representing the group 2 fibre input to striate cells. However, the mean OX-OR latency difference (1.05 msec) and the mean OR conduction

time (0.5 msec) of fibres projecting to area 18 (Chapter 2) are similar to the OX-OR and OR latencies of group 1 axons afferent to area 17 (1.2 and 0.63 msec respectively). These results are therefore in agreement with previous reports which indicate that Y cells innervate both area 17 and area 18 while X cells project only to area 17 (Garey and Powell, 1971; Stone and Dreher, 1973; Singer *et al.*, 1975; Hollander and Vanegas, 1977; LeVay and Ferster, 1977). Striate cells with OR latencies less than 2.0 msec (regarded as being monosynaptically activated) are concentrated in lamina IV and lamina VI. This finding is consistent with anatomical studies that show the dLGN axons terminating predominantly in these two laminae (cf. Fig. 2).

Cells in the S family (S and S_H) are less commonly excited than cells in either the C or B families. This result is at first sight, somewhat surprising given that simple cells have long been regarded as the first order neuron in the striate cortex (Hubel and Wiesel, 1962). However, although only 37% of S cells were activated from the optic radiation, they still constitute the largest absolute number of directly driven cells in the striate cortex (Fig. 11). Indeed 64% of all S cells excited from the optic radiation have latencies consistent with monosynaptic activation by thalamic afferents.

About 60% of S cells with OR latencies less than 2.0 msec have latencies that lie between 1.5 and 2.0 msec (Fig. 11). Very few monosynaptically excited parastriate neurons have OR latencies in this range (Fig. 9) and it would seem therefore that S cells generally receive relatively more slowly conducting

geniculocortical fibres. In addition, the receptive field properties of S cells suggests that they receive a substantial inhibitory input. The proportion of monosynaptically driven S cells is therefore likely to be significantly higher than the present results suggest. The OX and OR latencies of S cells do indicate that a number of S cells are directly innervated by fast conducting (brisk transient or Y type) fibres. However, the fast afferent system, unlike the slow stream, is readily activated by electrical stimulation (cf. METHODS). In reality therefore, it is highly probable that the proportion of S cells driven by fast fibres is relatively small. A few S cells have OX/OR latencies indicative of indirect activation by thalamic afferents and the two cells shown in Fig. 12 appear to be driven by fast conducting fibres. It is not clear whether S cells are also indirectly excited by fibres of the slow geniculocortical stream.

In terms of the heirarchical concept (Hubel and Wiesel, 1962, 1965) simple or S cells might be expected to be the only cells monosynaptically activated by stimulation of geniculocortical axons. From the analysis of OR and OX latencies this does not appear to be the case and perhaps the most potent example of this inconsistency is that S_H cells, which because of their hypercomplex property would be placed at the final stage in a heirarchical sequence, are found to have response latencies compatible with monosynaptic activation. Like the S cell, some S_H cells appear to be activated by fast and others by slowly conducting thalamic afferents. The response latencies of some S_H cells are indicative of polysynaptic

activation (cf. Fig.11) but it is possible that cells of this type are difficult to drive with electrical stimulation because they are much more selective in respect to their visual stimulus requirements. Thus polysynaptically driven S_H cells are almost certainly more common than indicated by the present results. As might be expected from the laminar distribution these less responsive S_H cells usually occur in laminae II and III.

About half of all the B and C cells recorded in area 17 are excited from the optic radiation. This proportion is higher than for S and S_H cells and may indicate that B and C cells often receive fast conducting afferents. Alternatively it is possible that cells of this kind are less influenced by inhibitory pathways. As a result, electrical stimulation of the slow conducting system would probably be more successful in C and B cells.

Of the C cells driven from OR, 67% have latencies less than 2 msec. As shown in Fig. 11 the majority of these presumed monosynaptic latencies are less than 1.5 msec. This is in direct contrast to the OR latencies of cells in the S family and indicates that many C cells are innervated by fast conducting fibres. Consistent with this, four C cells excited from both OX and OR have latencies within the monosynaptic reference circle for group 1 fibres (Fig. 12). No C cells have latencies indicative of direct activation by group 2 or X-type geniculocortical fibres. Some C cells are indirectly driven from the optic radiation and this input appears to be mediated by either the fast or the slow stream. The high

proportion of electrically excitable C cells thus appears to be related to the fact that these cells commonly receive a fast conducting input. However, as for cells in the S family, the absence of excitation in a number of cells of the C type may indicate that they are innervated (whether directly or indirectly) by more slowly conducting afferent axons.

Although B cells are commonly activated from the optic radiation, only 26% of the cells driven from OR have latencies less than 2.0 msec. This suggests that few B cells receive a direct input from either the slow or the fast streams. Of the cells stimulated from both OX and OR, none are found in the group 1 or group 2 monosynaptic reference circles and the majority have latencies indicative of indirect activation by geniculocortical fibres. The OX-OR latency differences are 1.5 msec or more which may indicate that slow conducting fibres are mediating the input to these striate neurons (cf. Fig. 12).

With regard to other striate receptive field types, no B_H or C_H cells have OR latencies less than 2.0 msec. The one C_H cell stimulated from both OX and OR has latencies suggestive of indirect activation by group 1 afferents. In contrast almost all of the non-oriented and concentrically organised cells have OR latencies consistent with direct excitation by geniculocortical fibres. As shown in Fig. 12 all non-oriented units driven from OX and OR are found in the monosynaptic reference circle representing group 2 (or brisk sustained) afferents.

In summary, the results indicate that the S cell is commonly the first order neuron in the striate cortex. This

is consistent with the observation that this cell class is concentrated in the thalamic receiving layers, laminae IV and VI. S cells can receive either fast or slow afferent fibres although it appears that the latter input predominates. Some S_H cells are also excited monosynaptically by either fast or slowly conducting geniculocortical fibres. A number of C cells are directly innervated by thalamic afferents but in contrast to S cells this input seems restricted to the fast system. There is little evidence to support direct activation of C cells by more slowly conducting axons. The latencies of B cells are in general indicative of indirect activation by either fast or more commonly slow fibres. Finally, non-oriented and concentric units are invariably monosynaptically excited by incoming geniculocortical axons.

Stone and Dreher (1973) have suggested that simple and complex cells in area 17 are driven by X and Y geniculate cells respectively. In contrast, Singer *et al.* (1975) have reported that individual simple and complex cells can receive either X or Y afferents. The present results provide some support for both conclusions. In agreement with Singer *et al.* (1975) it is clear that S cells can receive either fast or slowly conducting geniculate fibres. However, it would seem that by far the majority of S cells are innervated by more slowly conducting axons (cf. Stone and Dreher, 1973). C and B cells would presumably be included in the complex category of both Stone and Dreher (1973) and Singer *et al.* (1975). A significant number of C cells are innervated (either directly or indirectly) by fast conducting thalamic afferents. This result is in

agreement with both Stone and Dreher (1973) and Singer *et al.* (1975). The observation that a number of C cells receive a direct input is surprising given that this cell type is encountered rarely in laminae IV and VI. However, the number of monosynaptically driven C cells is likely to be small when compared to S cells. It may be that C cells (and perhaps cells in other receptive classes) in laminae III and V have access to incoming afferent information by way of apical or basal dendrites that extend into lamina IV.

Very few C or B cells are directly excited by slowly conducting geniculate fibres. This result is similar to Stone and Dreher (1973) but contrasts with Singer *et al.* (1975) who found that 30% of complex cells are monosynaptically driven by X-afferents. However, there are indications that both C and more commonly B cells are indirectly driven by these slow fibres.

Toyama, Maekawa and Takeda (1977) have also shown that simple and complex cells are monosynaptically driven by thalamic afferents. However, it is not clear what type of afferent fibre innervates the two cell classes. Further, Toyama, Kimura, Shiida and Takeda (1977) have reported that both complex and hypercomplex cells receive disynaptic excitation from geniculate fibres. From the present results C_H and B_H cells often have latencies suggestive of indirect activation but a significant number of S_H cells are monosynaptically driven from the optic radiation.

The considerations discussed above provide no clear

indication as to whether the separate geniculocortical streams are kept apart in the striate cortex. There is an indication that many C and S cells receive fast and slow conducting axons respectively, however the distinction is by no means absolute. Indeed although cells in the S family are commonly innervated by X-type fibres, they also receive inhibitory inputs which are mediated by the fast conducting system. Furthermore, it has been tacitly assumed that individual cells are excited by one type of geniculate afferent or the other but not by both. The experiments of Lee, Cleland and Creutzfeldt (1977) show that both a sustained and a transient ganglion cell can project to the same striate simple cell. It is not known how frequently this occurs, but excitatory convergence of this kind makes much of the parallel processing argument redundant.

A major problem in attempting to assess the connectivity of cells in the striate cortex is that many cells are not excited by electrical stimulation. This lack of excitation precludes a detailed analysis of the way information is processed in area 17, especially when extracellular recording techniques are used. In many ways, area 18 is more suited for a study of this type since it receives a heavy projection from fast conducting geniculate fibres and is therefore less subject to inhibitory effects. Such a study is described in the following chapter.

CHAPTER TWO

THE AFFERENT CONNECTIONS AND LAMINAR DISTRIBUTION OF CELLS IN AREA 18

INTRODUCTION

Hubel and Wiesel (1962, 1965) were the first to show, using single unit techniques, that there were three topographically organized visual areas of the cat coexistent with three separate cytoarchitectonically defined cortical regions. Using the histological maps of Otsuka and Hassler (1962), Hubel and Wiesel (1962, 1965) showed that the physiologically identified regions visual I, visual II and visual III corresponded to areas 17, 18 and 19 respectively. It was their contention that area 17 was the only region which received afferents from the dorsal lateral geniculate nucleus (dLGN) of the thalamus and the striate cortex was therefore regarded as the primary visual area of the cat. The more laterally placed areas 18 and 19 were thought to be secondary visual areas having no direct access to visual information passing up through the thalamus.

Even before these studies of Hubel and Wiesel however, there was evidence that the lateral visual areas of the cat might, to some extent, function independently of area 17. Thus both Talbot (1942) and Doty (1958) were able to record responses to visual stimulation in the lateral part of the lateral gyrus of the cat after removal or pharmacological disruption of more medial parts of the cortex. The advent of modern neuroanatomical research methods has since shown that the dLGN of the cat, unlike that of monkey and man, does indeed send axons to areas 18 and 19 as well as to the striate cortex (area 17).

The projection to areas 18 and 19 of the cat has been shown anatomically using degeneration (Garey and Powell, 1967;

Glickstein, King, Miller and Berkley, 1967; Wilson and Cragg, 1967; Niimi and Sprague, 1970; Burrows and Hayhow, 1971; Garey and Powell, 1971) and autoradiographic (Rosenquist, Edwards and Palmer, 1974; LeVay and Gilbert, 1976) techniques and by the method of retrograde transport of horseradish peroxidase (HRP) (Gilbert and Kelly, 1975; Maciewicz, 1975; Garey and Blakemore, 1977; Hollander and Vanegas, 1977; Kennedy and Baleydier, 1977; LeVay and Ferster, 1977).

Of particular relevance to the present study are reports which have described the thalamic input to area 18. After lesions in the dLGN, Garey and Powell (1971) reported that the efferent geniculocortical fibres to area 18 of the cat were considerably coarser than those to area 17. This result was related to the observation that small and large cells of the dLGN send axons to area 17, whereas only large cells project to area 18 (Garey and Powell, 1967). The suggestion that area 18 of the cat is predominantly innervated by the larger geniculocortical fibres has recently received support from HRP studies. Thus, after an injection of HRP into area 18, labelling in lateral geniculate neurons is mainly confined to the larger cells (Gilbert and Kelly, 1975; Garey and Blakemore, 1977; Hollander and Vanegas, 1977; LeVay and Ferster, 1977) and these neurons are found most often in laminae A1 and C (Hollander and Vanegas, 1977; LeVay and Ferster, 1977). Large somata are generally thought to give rise to large axons (cf. Wässle, Levick, Kirk and Cleland, 1975) hence the HRP studies confirm that the majority of geniculocortical fibres projecting to area 18 are of large diameter.

In addition to the projection from the dLGN, area 18 also receives a significant input from the medial interlaminar nucleus (MIN) (Glickstein *et al.*, 1967; Niimi and Sprague, 1970; Burrows and Hayhow, 1971; Rosenquist *et al.*, 1974; Maciewicz, 1975; Kennedy and Baleydier, 1977). HRP studies indicate that, as in the dLGN, it is the larger cells in MIN which give rise to the thalamocortical fibres (Gilbert and Kelly, 1975; Garey and Blakemore, 1977; Hollander and Vanegas, 1977; LeVay and Ferster, 1977). There is some disagreement as to whether the more medial thalamic nuclei (pulvinar complex (PUL), lateral posterior nucleus (LP), and posterior nucleus (PN)) also send axons to area 18. Some studies have indicated that of the three areas, only PUL projects to area 18 (Gilbert and Kelly, 1975; Maciewicz, 1975; Kennedy and Baleydier, 1977), whereas other reports suggest that LP is the origin of these extrageniculate thalamocortical fibres (Niimi and Sprague, 1970; Hollander and Vanegas, 1977). Whatever the exact location of the cells in the medial thalamic complex which send axons to area 18, the projection is sparse and it is apparent that most of the input to cat parastriate cortex arises from the large cells of the dLGN (especially laminae A1 and C) and from MIN.

The observation that area 18 is innervated by large axons suggests that the thalamocortical fibres projecting to this region are fast conducting. Support for this proposition has come from studies in which cortical units in area 18 were orthodromically activated from the optic radiation (OR) and optic chiasm (OX) (Toyama and Matsunami, 1968; Stone and Dreher, 1973; Tretter, Cynader and Singer, 1975). The latency differences between OR and OX stimulation for area 18 neurons receiving

primary afferents are in the order of 1.0 to 1.5 msec, which is consistent with the suggestion that geniculo-parastriate axons are generally fast conducting.

Recording in the dLGN, Stone and Dreher (1973) have reported that only cells with short antidromic latencies are activated after electrical stimulation of area 18. In accord with the observation that Y-type (Hoffmann, Stone and Sherman, 1972; Wilson, Rowe and Stone, 1976) or brisk transient neurons (Cleland, Dubin and Levick, 1971; Cleland, Levick, Morstyn and Wagner, 1976) have the fastest conducting axons, all of the cells in the dLGN which project to area 18 have Y-type receptive fields (Stone and Dreher, 1973). As pointed out previously, most of the cells which send axons to area 18 have large cell bodies and are found most commonly in layers A1 and C of the dLGN and in MIN. It has been suggested (Wilson *et al.*, 1975; LeVay and Ferster, 1977) that the large cells in the dLGN are Y cells. Physiologically, Y cells or brisk transient cells are commonly recorded in layer C of the dLGN (Cleland *et al.*, 1976; Wilson *et al.*, 1976) as well as in MIN (Mason, 1975; Dreher and Sefton, 1978). These results taken with the results of Stone and Dreher (1973) described above, indicate that Y-type cells are likely to contribute the greater part of the projection to area 18.

With regard to the laminar distribution of the thalamic afferents in area 18, geniculocortical axons are found to terminate most commonly in lamina IV, to some extent in lamina VI, and rarely in laminae I, II, III and V (Garey and Powell, 1971; Rosenquist *et al.*, 1974; LeVay and Gilbert, 1976).

All the geniculocortical fibres which terminate in area 18 have asymmetric terminals and most synapse on dendritic spines (Garey and Powell, 1971; LeVay and Gilbert, 1976).

Since area 18 predominantly receives large rather than small fibres and since fast thalamic afferents are relatively easy to drive from both the optic radiation and optic chiasm (Singer and Bedworth, 1973; Stone and Dreher, 1973; Tretter *et al.*, 1975), it is often possible to define the conduction velocity of thalamocortical fibres which innervate parastriate cortical neurons. Thus, assuming the OR-OX latency difference is consistent with a fast input, any variation in the *absolute* orthodromic latencies of area 18 cortical units after OX and OR stimulation must result from effects within the cortex itself rather than from variability in the conduction velocity of afferent fibres. Using this latency data, it is then possible to place parastriate neurons in various classes depending on whether they are directly or indirectly innervated by thalamocortical axons. By correlating this information with the visual properties and laminar position of the cells, one can begin to analyse how incoming signals are processed within the visual cortex. Area 18 is particularly suitable for a study of this kind because of the unique nature of its thalamic input.

In summary, the present work has three major aims. The first is to study the receptive field properties of neurons in area 18 and to examine the laminar distribution of the different cell types. In the second part of the study, electrical stimulation of OR and OX has been used to determine the ordinal position of area 18 neurons with respect to the

geniculocortical input. The laminar distribution of cells directly or indirectly activated from the thalamus is compared to the distributon of afferent fibres derived from anatomical studies. Thirdly, the receptive field properties of area 18 cells are compared with their position with respect to the thalamic input, derived from electrical stimulation. From these results, a tentative model is put forward which attempts to show how incoming visual information is elaborated within area 18.

METHODS

The methodological procedures used in these experiments have been described in detail in the previous chapter. The data are taken from experiments performed on 24 adult cats. In 18 of these animals, stimulating electrodes were placed in the optic chiasm (OX) and optic radiation (OR) (cf. Chapter 1). The two pairs of electrodes were positioned stereotaxically and field potentials recorded in area 18 were used to check that the electrodes were at the optimal depth. A diagrammatic representation of the position of the OX and OR stimulating electrodes is presented in Fig. 1.

As in the previous chapter, an unambiguous understanding of the disposition of laminae in area 18 is critical for the interpretation of the present results. An example of a Nissl-stained section of area 18 is shown in Fig. 2 and the scheme of lamination used in the present study is described below.

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

Lamina II-IIIa: Both Otsuka and Hassler (1962) and Garey (1971) have described layer II as being predominantly composed of small pyramidal cells. The presence of these small cells can be clearly seen in Fig. 2. This superficial region has been termed 'II-IIIa' in the present study since it is difficult to determine exactly where layer II ends and layer III begins.

Lamina III: The broadness of lamina III is perhaps the most significant cytoarchitectonic feature of the parastriate cortex. Garey (1971) has reported that the lower aspect of layer III is

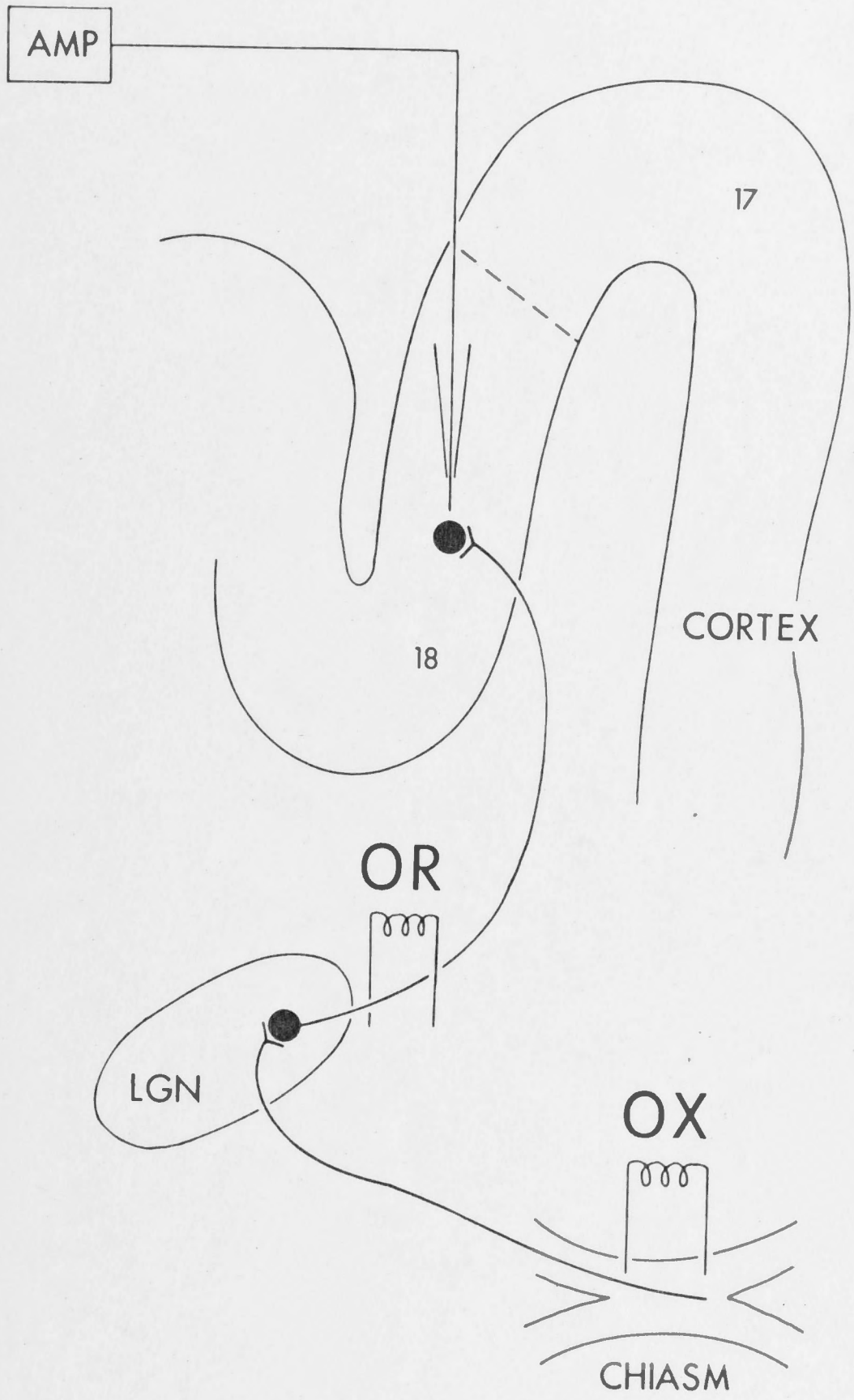
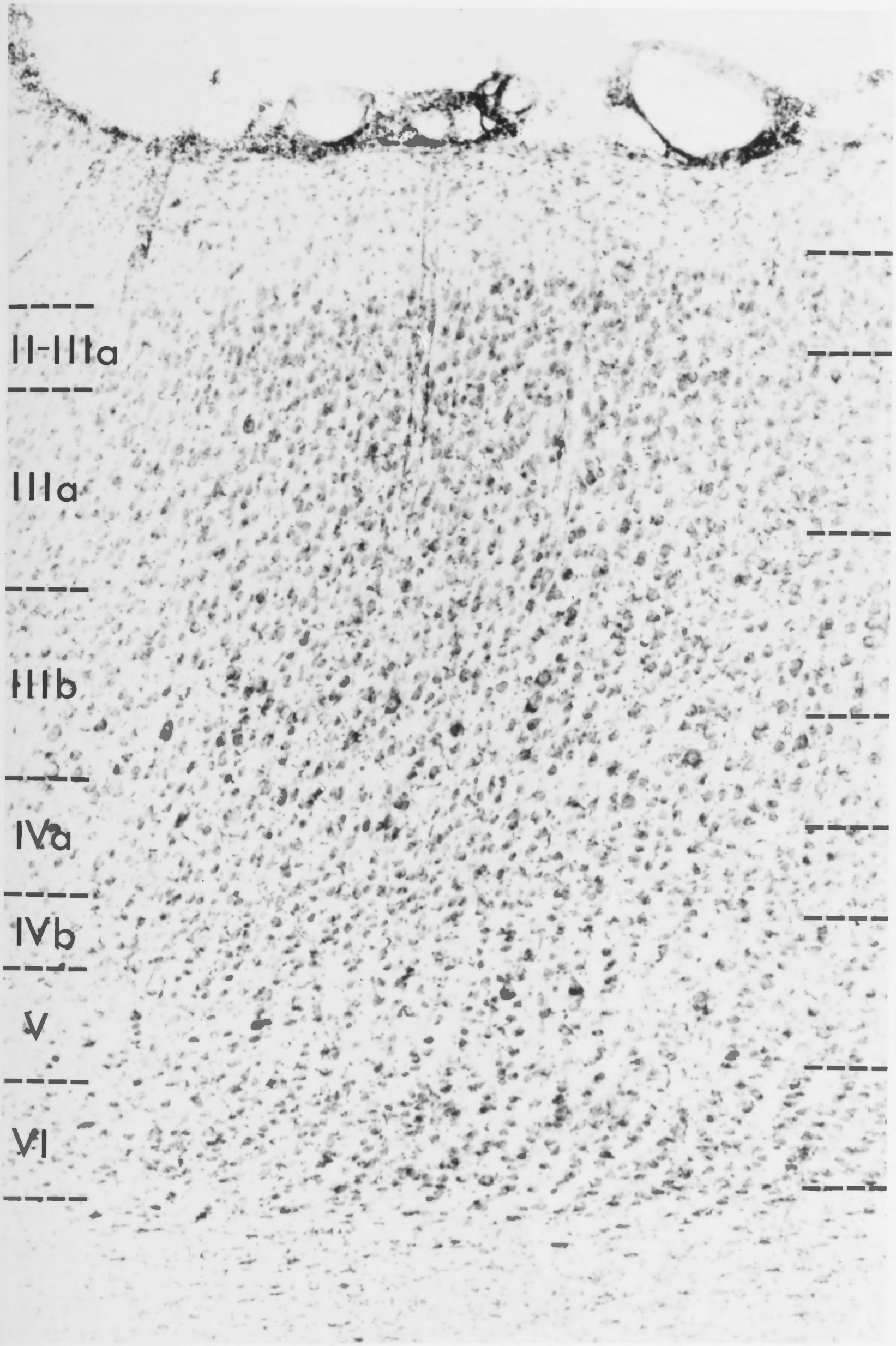


Fig. 1. Schematic representation of the experimental arrangement employed in the present study. OR and OX, stimulating electrodes positioned in the optic radiation and optic chiasm. LGN, lateral geniculate nucleus.

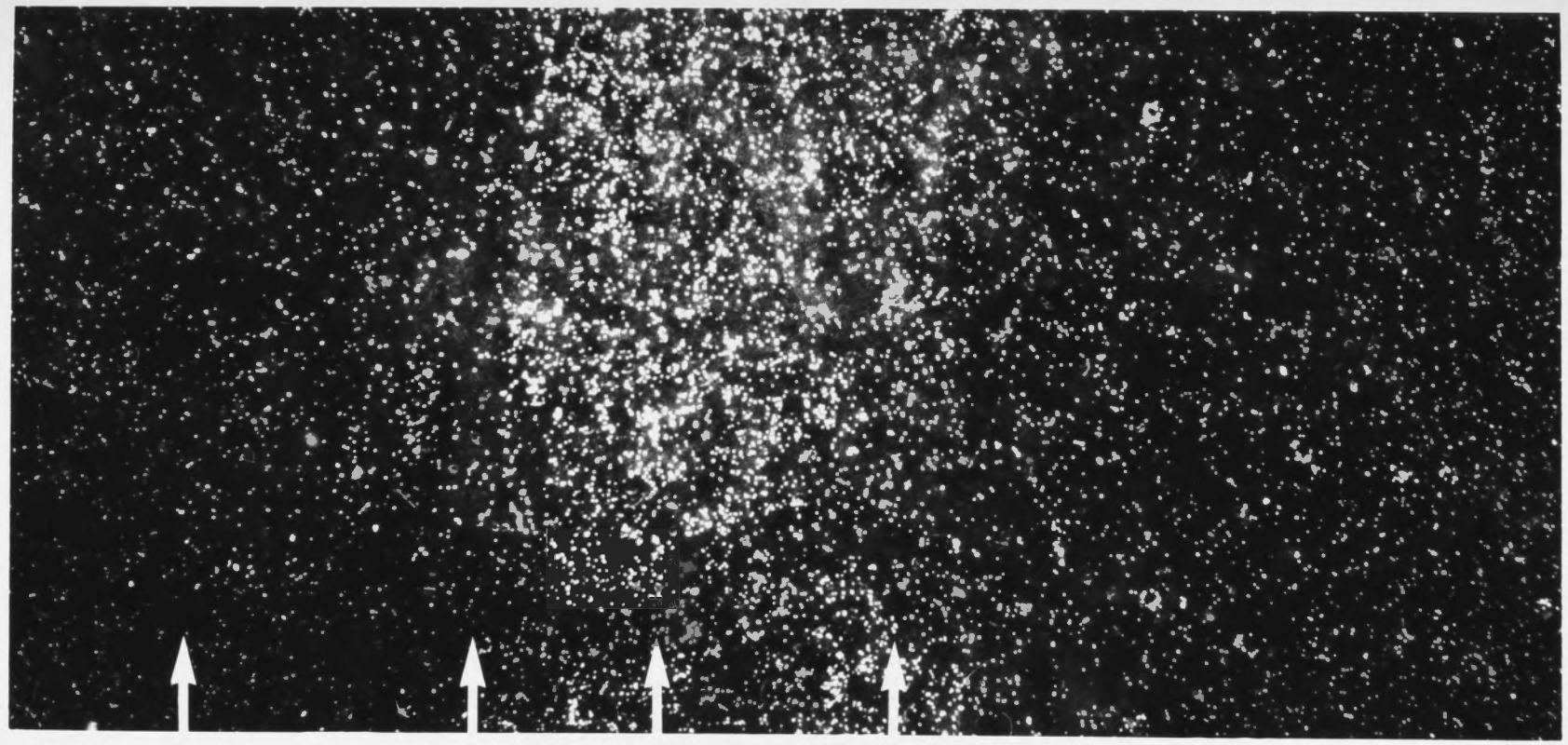
Fig. 2. Photomicrograph of Nissl-stained section showing the disposition of laminae in area 18 of the cat. The area of cortex shown here lay in the lateral bank of the lateral gyrus.

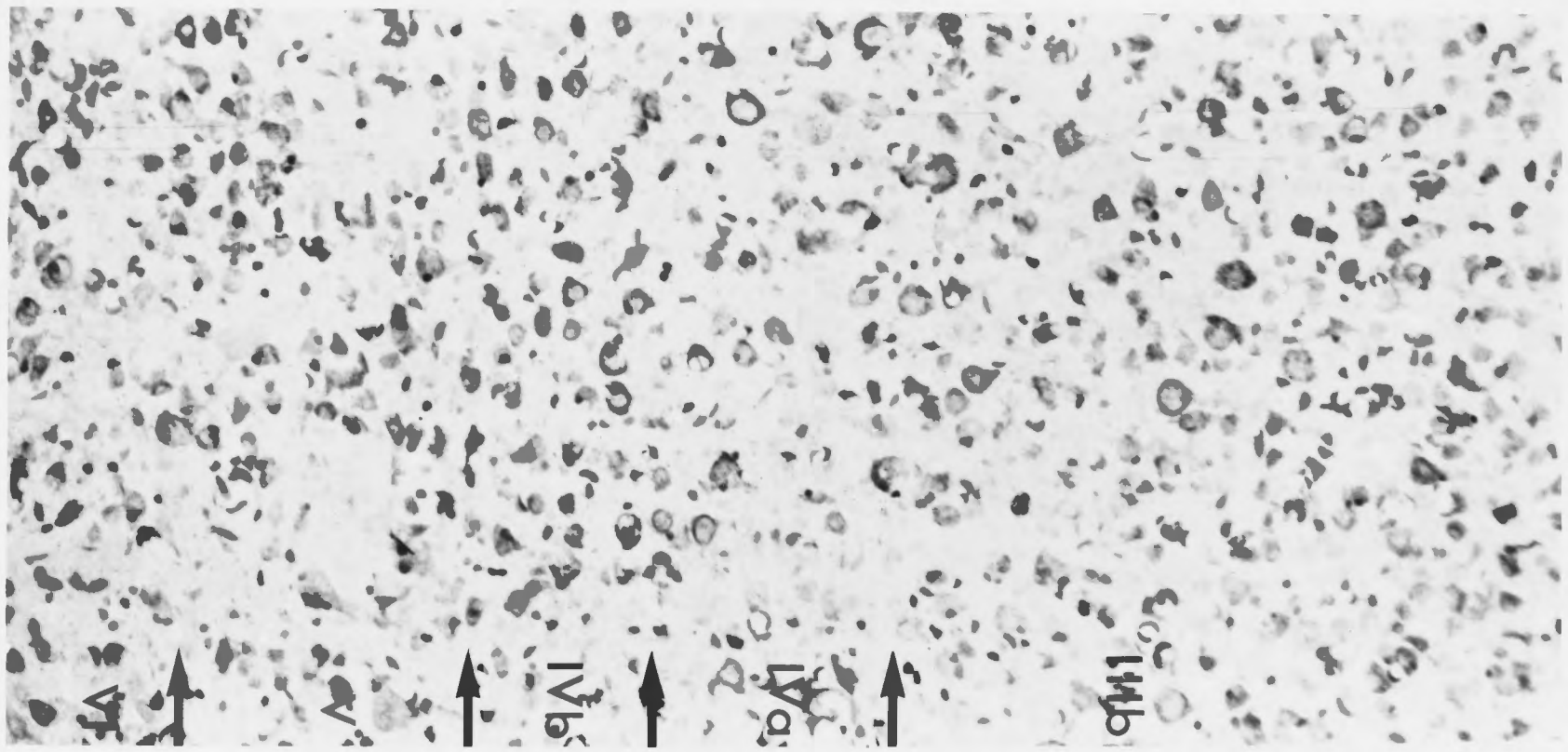

II-IIIa
IIIa
IIIb
IVa
IVb
V
VI

situated about half way through the thickness of the cortex. Otsuka and Hassler (1962) subdivided this lamina into two parts: IIIa and IIIb. IIIa is composed of small to medium-large pyramids while IIIb contains a mixture of large, medium and small cells. The increase in the size of pyramidal neurons is evident in Fig. 2. To assist in the analysis of the afferent connectivity of area 18, layer III has also been divided into two parts (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: Garey (1971) describes lamina IV as being narrow and not divisible into two distinct bands, while Otsuka and Hassler (1962) comment that the layer is loosely built out of relatively large granular cells. In the present study, in contrast to Garey (1971), lamina IV has been subdivided into two regions. Immediately below the large pyramidal cells (which are situated about half way through the cortex) 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. In the present study, this has been designated lamina IVb. Justification for regarding both these regions as being part of lamina IV comes from an experiment which examined the labelling in the parastriate cortex after an injection of (^{3}H) proline into the lateral geniculate nucleus. The procedures used in this autoradiographic experiment were identical to those described in Chapter 1. The results are presented in Fig. 3.

Fig. 3. Radioactive labelling in the parastriate cortex resulting from an injection of (^{3}H) proline into the dorsal lateral geniculate nucleus. 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.




IVb1
IVb2
IVb3
IVb4

The band of radioactivity clearly extends throughout both the loose (lamina IVa) and densely packed (lamina IVb) bands. Most of the labelling is confined to these regions and does not extend beyond the large pyramids in either lamina III or lamina V.

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 recognised 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. Both Rosenquist *et al.* (1974) and LeVay and Gilbert (1976) have reported that lamina VI of area 18 receives a weak but significant projection from the geniculate. Such a projection was not evident in the present autoradiographic study.

Generally, the recording electrode entered the cortex between Horsley-Clark posterior 1 and 5. All penetrations in area 18 passed down the lateral bank of the lateral gyrus and crossed the 17/18 border zone (Fig. 5). To extend the traverse of area 18, the electrode was tilted with its tip angled laterally by about 10^{o}. 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 Chapter 5. Only those units which were unambiguously located in area 18 have been included in the present analysis.

RESULTS

RECEPTIVE FIELD PROPERTIES OF AREA 18 NEURONS

Classification Scheme

Both moving and stationary stimuli were used to qualitatively examine the receptive fields of area 18 cells. The terminology of Henry (1977) (cf. Chapter 1), originally designed for area 17, has with some adaption 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. Of the 117 S cells for which edge regions were plotted, 40 (34%) responded to only one edge (27 to dark and 13 to light edge), 69 (59%) responded to both light and dark edges, and 8 (7%) had more than two edge response regions. Using moving stimuli, the mean separation of the primary borders (Bishop and Henry, 1972) of individual 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 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 (Camarda, in preparation) that quantitative analysis of receptive fields

sometimes reveals a second response region that is too weak to recognise using qualitative methods.

Forty-three S cells (37%) responded to 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 directional specificity.

When tested with stationary flashing stimuli, S cells can be subdivided into spatially separate ON and/or OFF areas. In the present study, it was found that narrow bars of light flashed on and off in the receptive field often evoked only weak responses in area 18 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 cells 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.

Thirty-nine (33%) S cells possessed only one stationary flashing light field; 13 units responded only to ON and 26 responded only to OFF. Fifty S cells (43%) 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 recognised. 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 (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.

Not all cells with spatially separate dark and light edge response fields have been classed as S. Very rarely (3 out of 223 visually responsive 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^{o}) 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 and Wiesel (1962). They have been designated as A cells in accordance with the classification scheme of Henry (1977).

C and B cells

A substantial number of parastriate neurons have spatially coincident light and dark edge response regions. In addition, they give mixed ON/OFF discharges over the entire receptive field when tested with stationary flashing stimuli. Cells with these properties have been divided into two basic categories.

(1) C cells have relatively large receptive fields (the mean separation of the primary borders was 4.7^{o}), they are broadly tuned for stimulus orientation and generally have a high rate of spontaneous activity. Their response 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 59 C cells encountered in the present study, 14 (24%) resembled the striate cells described by Palmer and 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 enhanced the response; in 12 cells, no response was obtained with small stimuli and very long edges (up to 10^{o}) were required for consistent activation.

Twenty-four C cells (42%) responded to only one direction of movement and 9 (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 required a lot of length summation (cf. Chapter 3).

(2) Units designated as B cells (Henry, Lund and Harvey, 1978) are similar to C cells in that their light and dark edge regions are superimposed and stationary stimuli elicit mixed ON/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 quite sharply tuned for stimulus orientation. B cells do not appear to be as common in area 18 as in area 17 (Chapter 1) and it should be added that the distinction between parastriate C and B cells is not as clear as in the striate cortex.

The H property

Some S, C and B cells respond 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 (Hubel and Wiesel, 1965) or H cells and units exhibiting this property have been designated S_H, C_H and B_H (Henry, 1977). In area 18, end-zone inhibition is rarely strong enough to completely suppress the response to an elongated stimulus. 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 (Rose, 1977; Kato, Bishop and Orban, 1978).

Non-oriented units

Forty-six units, recorded in the grey matter of area 18, were monocular and had concentric receptive fields typical of

geniculocortical afferent fibres. The central regions of these non-oriented units ranged from 0.7° to 2.7° in diameter and they typically responded best to fast stimulus movements. Of the afferent fibres for which receptive fields were plotted, 20 had ON and 19 had OFF centres. After optic radiation (OR) stimulation, these presumed 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. 11).

Rarely, non-oriented (N.O.) units were encountered which were activated post-synaptically after OR stimulation. A similar small number of non-oriented cortical cells has also been reported in area 17 (Chapter 1).

The relative proportions of area 18 cell classes

In 24 cats, 366 units were held long enough to allow a thorough search for their receptive fields. Of these units, 223 (61%) were visually responsive and could be unambiguously classed according to the criteria described above. The number of units in each cell class, and their relative proportions considered with regard to the total number of cells in the sample are shown in Table 1. S cells (33%), are the most commonly encountered receptive fields type in area 18 (cf. Tretter *et al.*, 1975; Orban and Callens, 1977a).

Stimulus velocity

As described by previous workers (Stone and Dreher, 1973; Dreher and Cottee, 1975; Tretter *et al.*, 1975; Orban, 1977; Orban and Callens, 1977a,b), area 18 cells generally prefer

TABLE 1

The encounter rates of parastriate cell classes

	RECEPTIVE FIELD CLASS									
	S	S_H	C	C_H	B	B_H	A	N.O.	NVC	TOTAL
NUMBER OF CELLS	119	13	59	14	8	3	3	4	143	366
% OF CELLS	32.5	3.6	16.1	3.8	2.2	0.8	0.8	1.1	39.1	100.0

NVC : Not visually classified

N.O.: Non-oriented

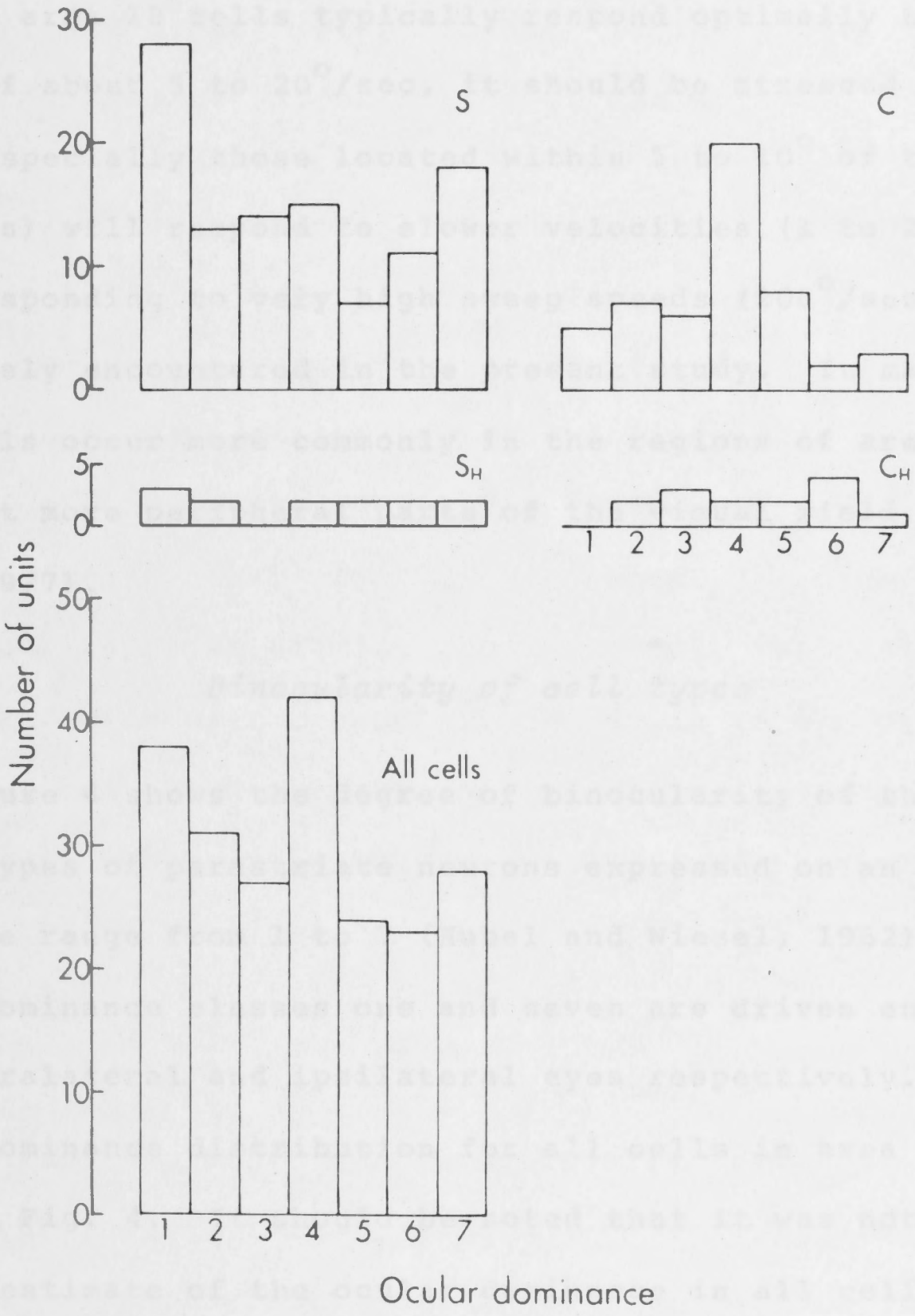


Fig. 4. Ocular dominance disribution for the four most common types of parastriate neuron and the overall distribution for all cells in area 18. Ocular dominance groups 1 and 7 represent cells driven solely from the contralateral and ipsilateral eyes respectively.

higher stimulus velocities when compared to striate neurons. Although area 18 cells typically respond optimally to stimulus speeds of about 5 to 20°/sec, it should be stressed that many cells (especially those located within 5 to 10° of the area centralis) will respond to slower velocities (1 to 2°/sec). Cells responding to very high sweep speeds (200°/sec or more) were rarely encountered in the present study. It may be that such cells occur more commonly in the regions of area 18 which represent more peripheral parts of the visual field (e.g. Orban, 1977).

Binocularity of cell types

Figure 4 shows the degree of binocularity of the four most common types of parastriate neurons expressed on an ocular dominance range from 1 to 7 (Hubel and Wiesel, 1962). Cells in ocular dominance classes one and seven are driven entirely by the contralateral and ipsilateral eyes respectively. The overall ocular dominance distribution for all cells in area 18 is also shown in Fig. 4. It should be noted that it was not possible to make an estimate of the ocular dominance in all cells. In addition, some cells which could not be satisfactorily placed in one of the receptive field classes, were nevertheless classified with regard to their ocular dominance. From Fig. 4, it is clear that more cells in the S family (both S and S_H cells) have a tendency to be monocularly activated than cells in the C family (C and C_H cells). Thus 44% of S type cells are driven by only one eye compared to 16% of cells in the C family. In addition, area 18 cells tend to be driven more often by the contralateral eye (45% in ocular dominance groups 1, 2 and 3) than by the

ipsilateral eye (35% in ocular dominance groups 5, 6 and 7) (cf. Hubel and Wiesel, 1965; Tretter *et al.*, 1975).

Receptive field classes and visual field eccentricity

All electrode penetrations in area 18 passed down the lateral bank of the lateral gyrus (Fig. 5) and so crossed the 17/18 border zone. Units in area 18 recorded close to this border regions have centrally located fields and receptive fields move out in a horizontal direction as the electrode moves deeper down the lateral bank (cf. Fig. 7, Chapter 5). Hubel and Wiesel (1965) have reported similar observations. The position of receptive fields with respect to elevation in the visual field depends on the anterior-posterior position of the electrode penetration. Most units in the present study had receptive fields within 5 or 6^{o} of the area centralis in the inferior visual field.

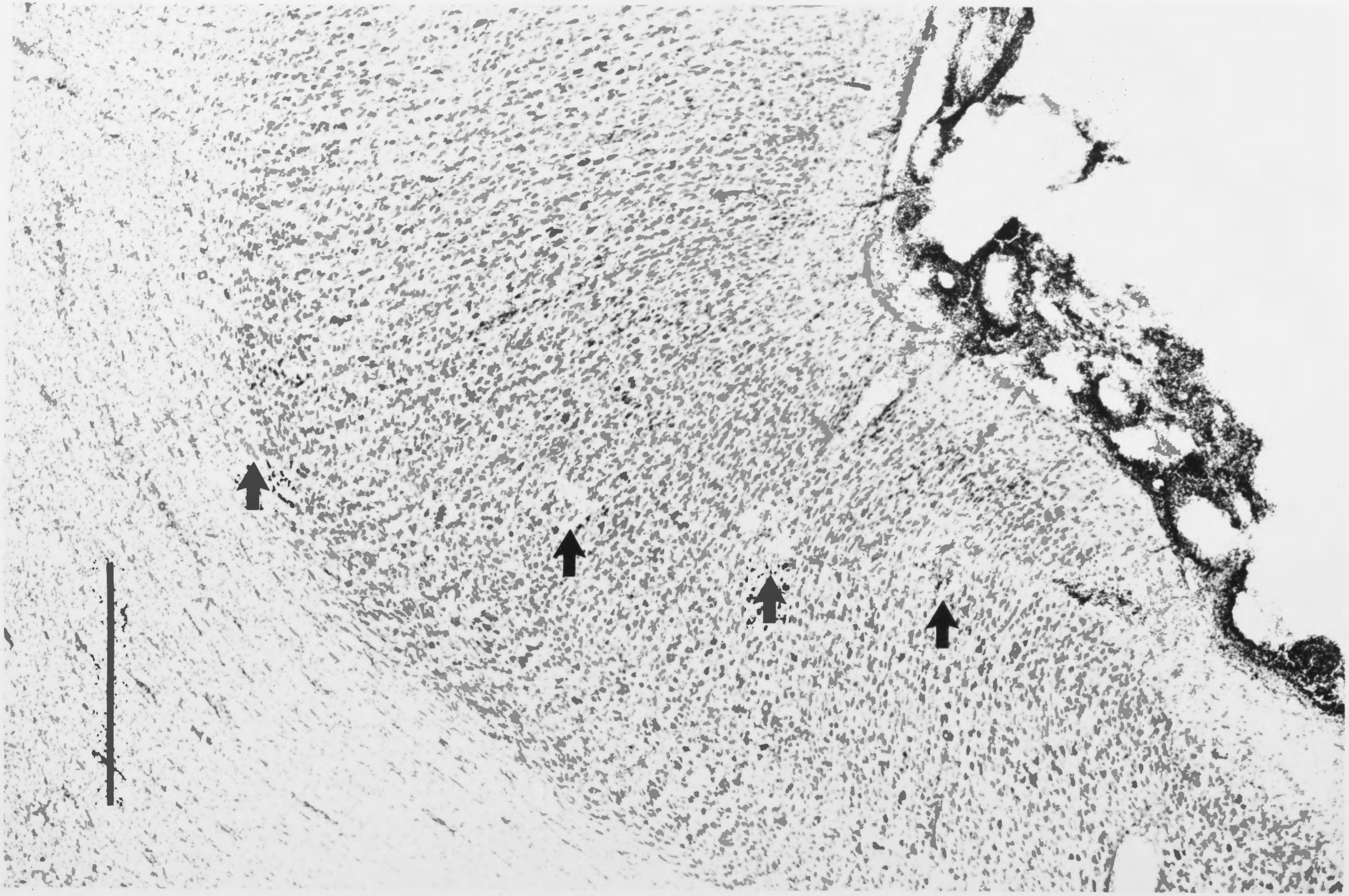
The visual field eccentricity of cells for which receptive fields could be plotted was determined by measuring the distance between the receptive field centre and the ophthalmoscopically estimated position of the area centralis; for binocularly driven units, the mean eccentricity for the two eyes has been used. One hundred and four cells had receptive fields located within 4^{o} of the area centralis and 122 had more peripheral fields. Cells with receptive fields within 4^{o} of the area centralis and cells with receptive fields at eccentricities greater than 4^{o} have been termed central and paracentral respectively (cf. Albus, 1975).

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 (S and S_H groups), 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 paracentral visual areas(cf. Hubel and Wiesel, 1965; Dreher and Cottee, 1975). The average separation of the primary borders of central C cells was 3.5^{o}, compared with 5.6^{o} 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 edge response fields was 0.87^{o} and 0.96^{o} in central and paracentral visual regions respectively.

The relative encounter rates of central and paracentral S and C cells were remarkably similar; S cells made up 51.9% and 51.6% of all cells located in central and paracentral visual fields respectively and 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 can be concluded that



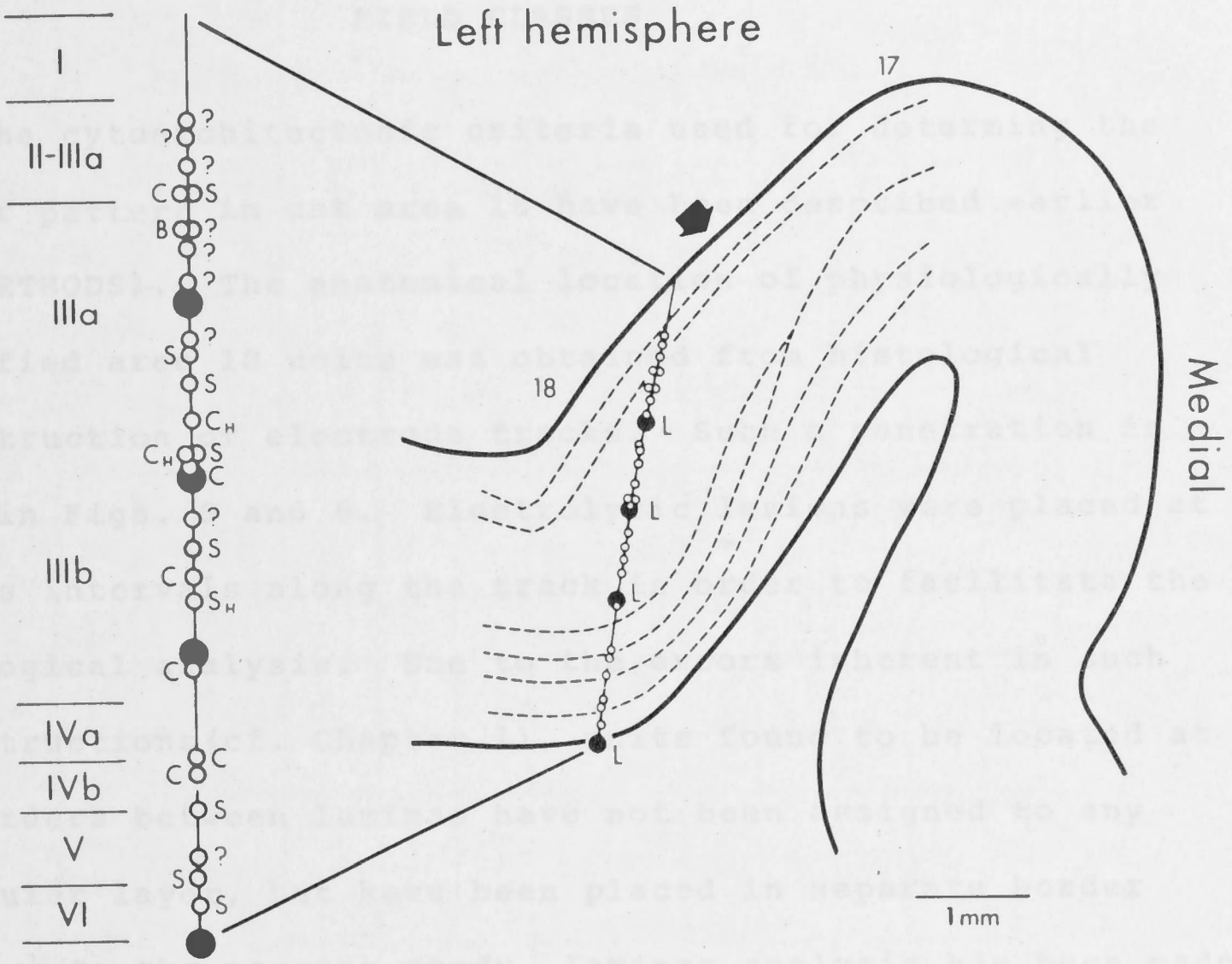


Fig. 5. (opposite) Photomicrograph of electrode penetration in the lateral bank of the lateral gyrus. The track is entirely within area 18. Arrows show the positions of electrolytic lesions. Marker respresents 1 mm.

Fig. 6. (above) Diagrammatic representation of the electrode track presented in Fig. 5 showing the location of single units recorded during the penetration. L, electrolytic lesions; arrow, 17/18 border region; ?, unclassified units.

S and C cells are distributed evenly throughout the visual representation in area 18 (at least up to eccentricities of 20°).

LAMINAR DISTRIBUTION OF RECEPTIVE FIELD CLASSES

The cytoarchitectonic criteria used for determing the laminar pattern in cat area 18 have been described earlier (see METHODS). The anatomical location of physiologically identified area 18 units was obtained from histological reconstruction of electrode tracks. Such a penetration is shown in Figs. 5 and 6. Electrolytic lesions were placed at various intervals along the track in order to facilitate the histological analysis. Due to the errors inherent in such reconstructions(cf. Chapter 1), units found to be located at the borders between laminae 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 on the 366 isolated cells and the 46 thalamocortical fibres is shown in Table 2. The data presented in Table 2 has been replotted in Fig. 7. In this figure, the proportions of the major cell types (expressed as a percentage of the total number of cells isolated in each layer) in each cortical lamina are shown. Such an analysis removes the effects of uneven sampling in different laminae. S cells occur most frequently in laminae IIIb, IVa and VI. In terms of the total number of S cells found in each layer, the proportions in which qualitative testing revealed only one

TABLE 2

Laminar distribution of receptive field classes in area 18

	RECEPTIVE FIELD CLASS										
LAMINA	S	S_H	C	C_H	B	B_H	A	N.O.	NVC	TOTAL	FIBRES
II-IIIa	3	1	4	3	1	1	0	0	32	45	0
IIIa	16	3	2	4	1	0	0	0	22	48	0
IIIb	24	6	11	0	1	1	0	0	18	61	3
IIIb/IVa	9	0	0	0	0	0	0	1	11	21	5
IVa	8	0	3	2	0	0	0	1	7	21	5
IVa/IVb	5	0	3	1	1	0	0	0	3	13	3
IVb	4	1	4	0	1	0	0	0	12	22	7
IVb/V	6	1	8	0	0	0	0	0	7	22	6
V	11	1	15	4	2	0	0	1	14	48	7
V/VI	5	0	2	0	0	0	1	0	3	11	4
VI	28	0	7	0	1	1	2	1	14	54	6

NVC : Not visually classified

N.O.: Non-oriented

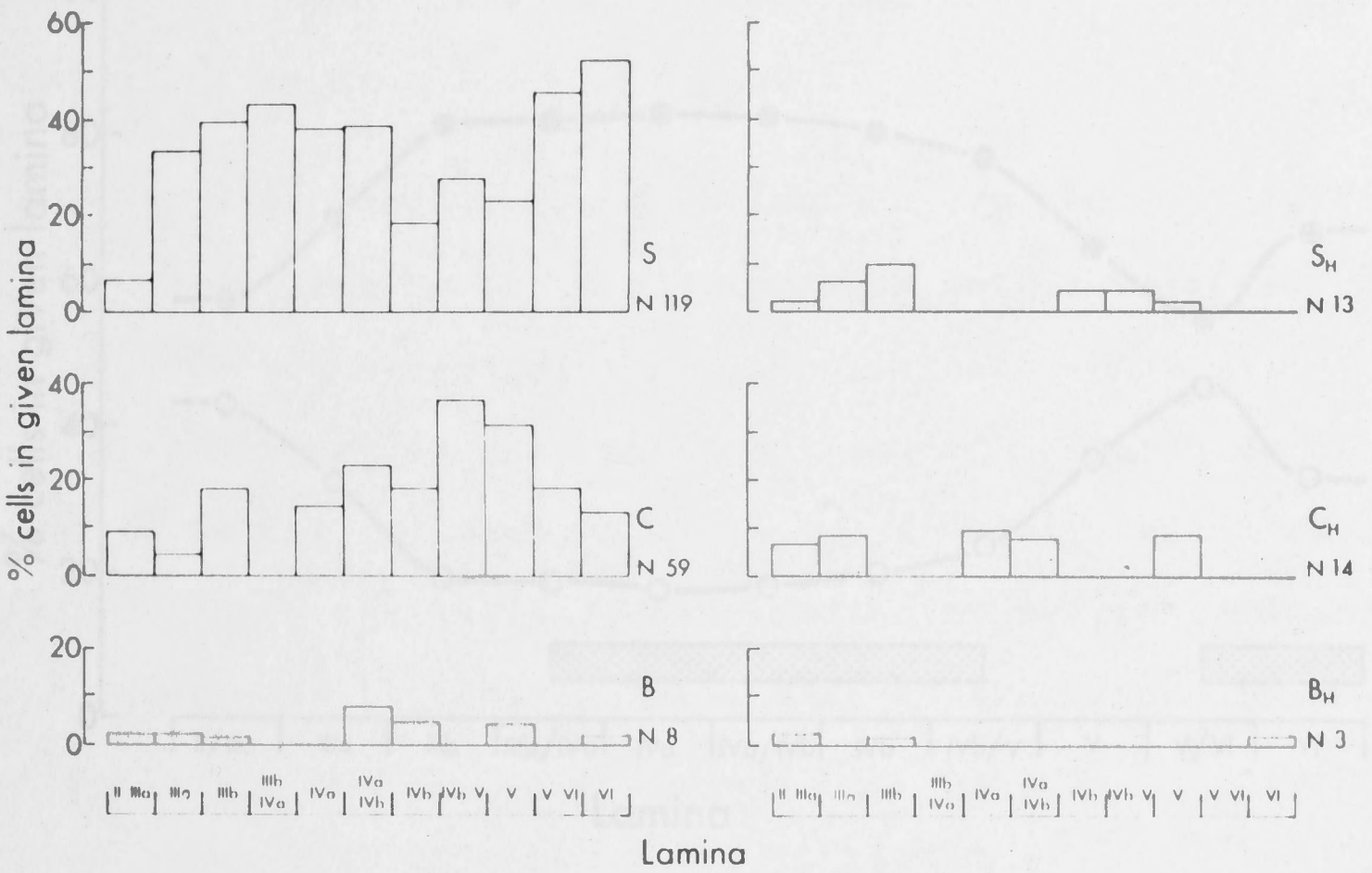


Fig. 7. Laminar distribution of the major cell types in area 18. For each cell type the proportions in each lamina are expressed as a percentage of the total number of cells encountered in that lamina.

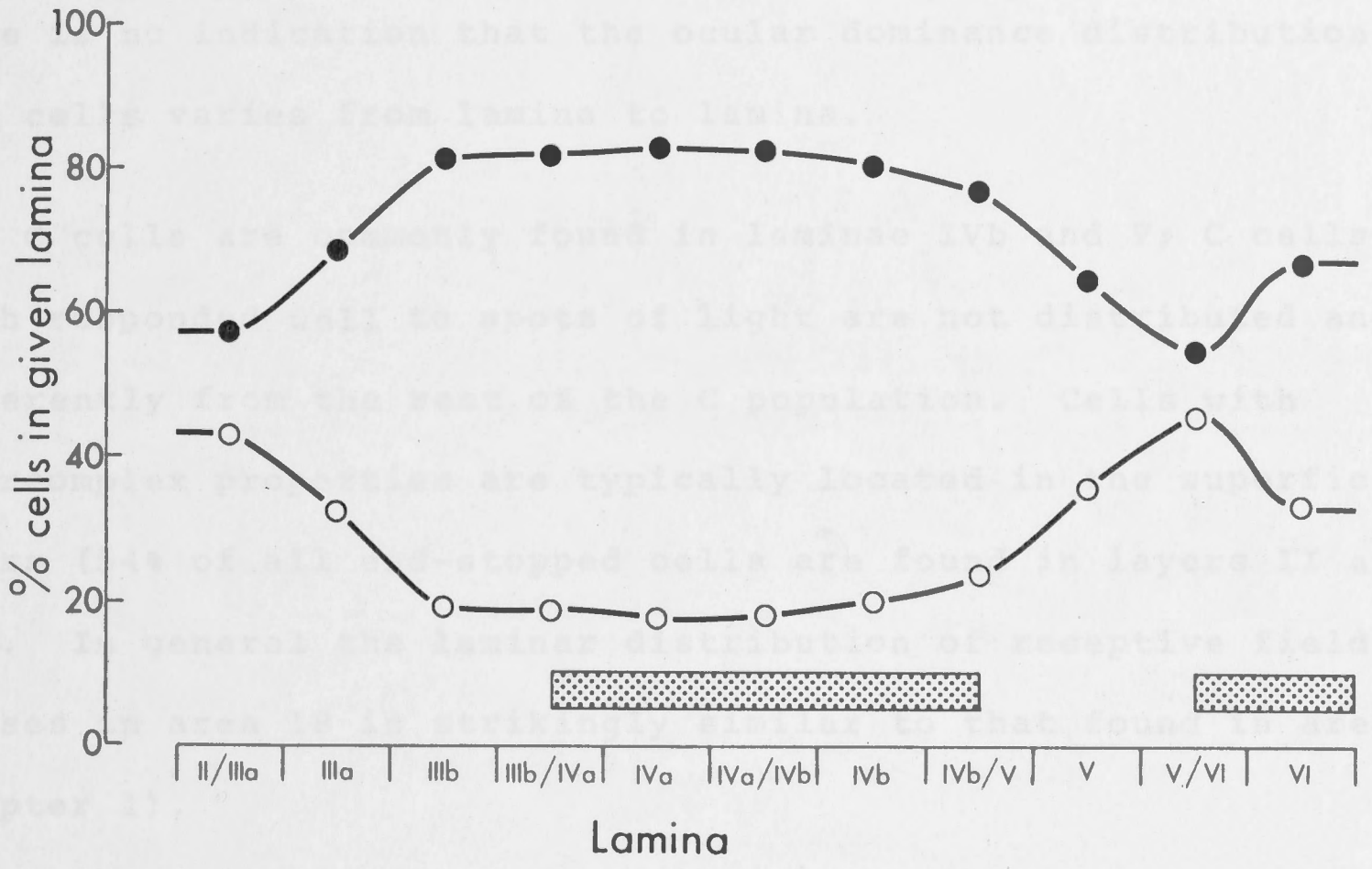


Fig. 8. The proportions of cells in each cortical lamina which were or were not orthodromically activated after optic chiasm (OX) and/or optic radiation (OR) stimulation. Filled circles, cells driven from OX and/or OR; open circles, cells not excited from either site; dotted blocks, laminae in which geniculocortical fibres terminate (demonstrated anatomically).

edge response region are highest in laminae IIIb, IVb and VI. On the other hand, S cells with only one ON or OFF area have a similar laminar distribution to those which have two or more stationary flashing light regions. Unlike area 17 (Chapter 1), there is no indication that the ocular dominance distribution of S cells varies from lamina to lamina.

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 typically located in the superficial layers (54% of all end-stopped cells are found in layers II and III). In general the laminar distribution of receptive field classes in area 18 is strikingly similar to that found in area 17 (Chapter 1).

THE THALAMIC INPUT TO AREA 18

General comments

Electrical stimulation of the optic radiation (OR) and optic chiasm (OX) was tested on 282 cells and 29 geniculocortical 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, 43 were excited from only OR and 6 were driven from only OX. Figure 8 shows the proportion of electrically excitable units in the different laminae of area 18. Cells located within a zone extending from laminae IIIb to IVb are more often activated after OX and/or OR stimulation than cells in more superficial and deeper layers. The dotted bars in Fig. 8 indicate the anatomically defined laminae in which thalamic afferents terminate (see METHODS).

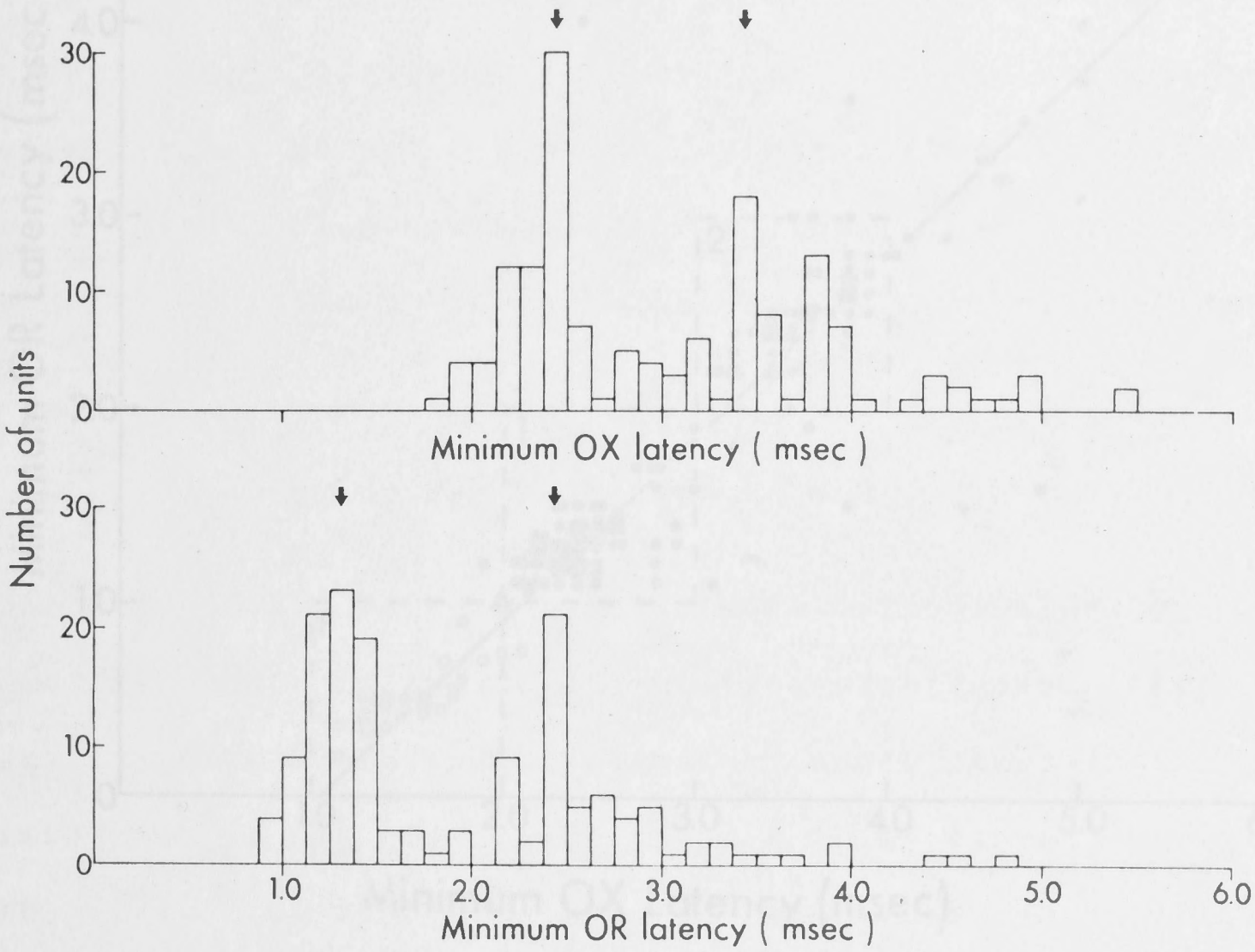


Fig. 9. Minimum orthodromic latencies of parastriate neurons excited by optic chiasm (OX) and optic radiation (OR) stimulation. Arrows indicate peaks in the latency distributions.

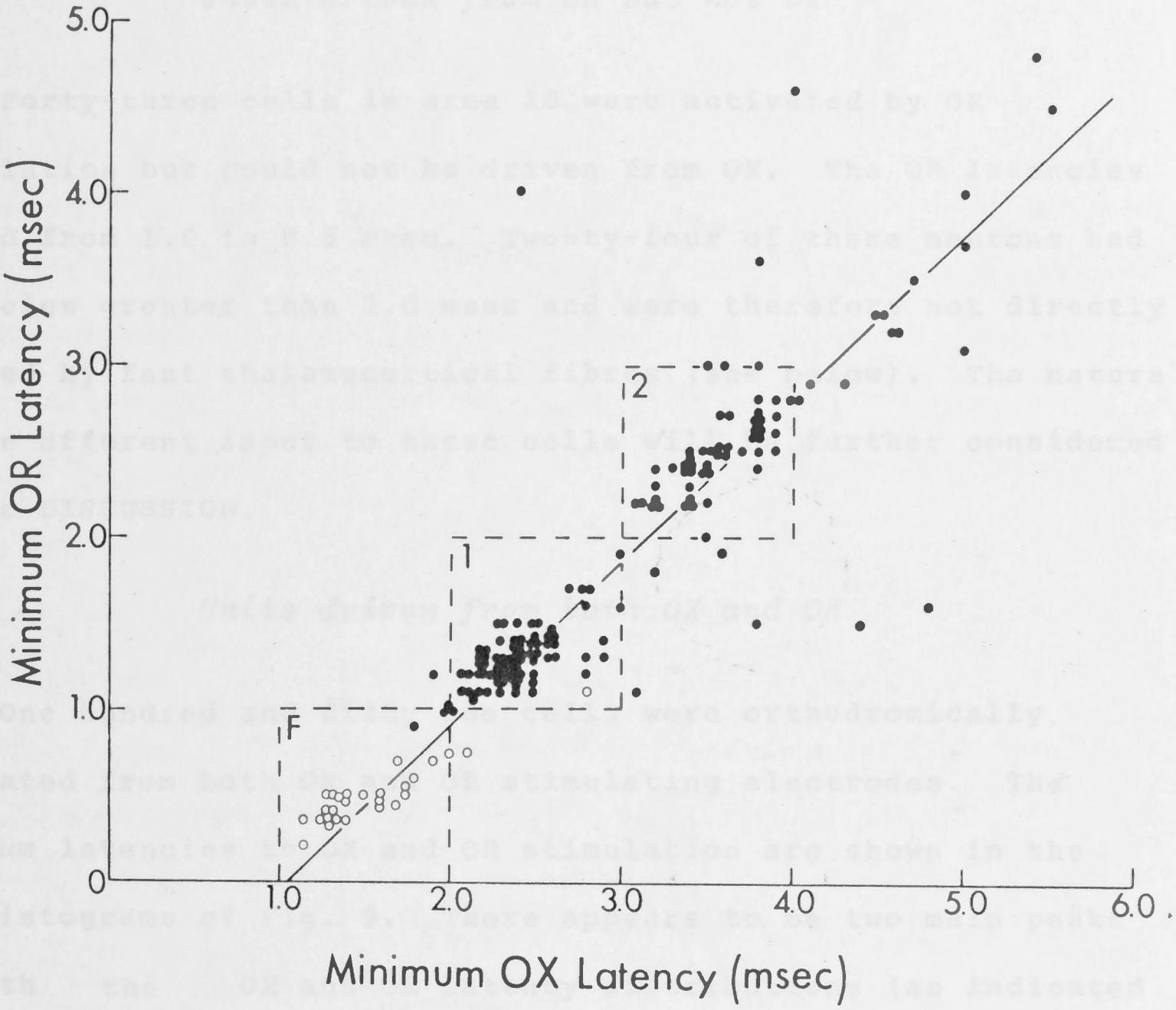


Fig. 10. Orthodromic optic chiasm (OX) and optic radiation (OR) latencies of parastriate neurons (filled circles) and geniculocortical fibres (open circles) recorded within the grey matter of area 18. The line represents the mean OX-OR latency difference (1.05 msec) of geniculocortical fibres and passes through all points at which the OX latency is equal to the OR latency plus 1.05 msec. Cells located within boxes 1 and 2 have been termed group 1 and group 2 respectively. Cells outside these areas are designated as group 3. Geniculocortical fibres are commonly found in the area marked F.

Units driven from OR but not OX

Forty-three cells in area 18 were activated by OR stimulation but could not be driven from OX. The OR latencies ranged from 1.0 to 8.5 msec. Twenty-four of these neurons 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 driven from both OX and OR

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. 9. There appears 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. 10, which presents the minimum latencies to both OX and OR stimulation for each cell (filled circles). Before analysing this data further however it is necessary to examine the OX and OR latencies of thalamocortical fibres recorded in the grey matter of area 18.

OX and OR latencies of geniculocortical fibres

The open circles in Fig. 10 show the OX and OR latencies for 27 geniculocortical fibres excited from both stimulating sites. An example of a geniculate axon excited by OX and OR stimulation is shown in Fig. 11. The minimum latencies to OX and OR stimulation were 1.4 and 0.42 msec respectively. Note

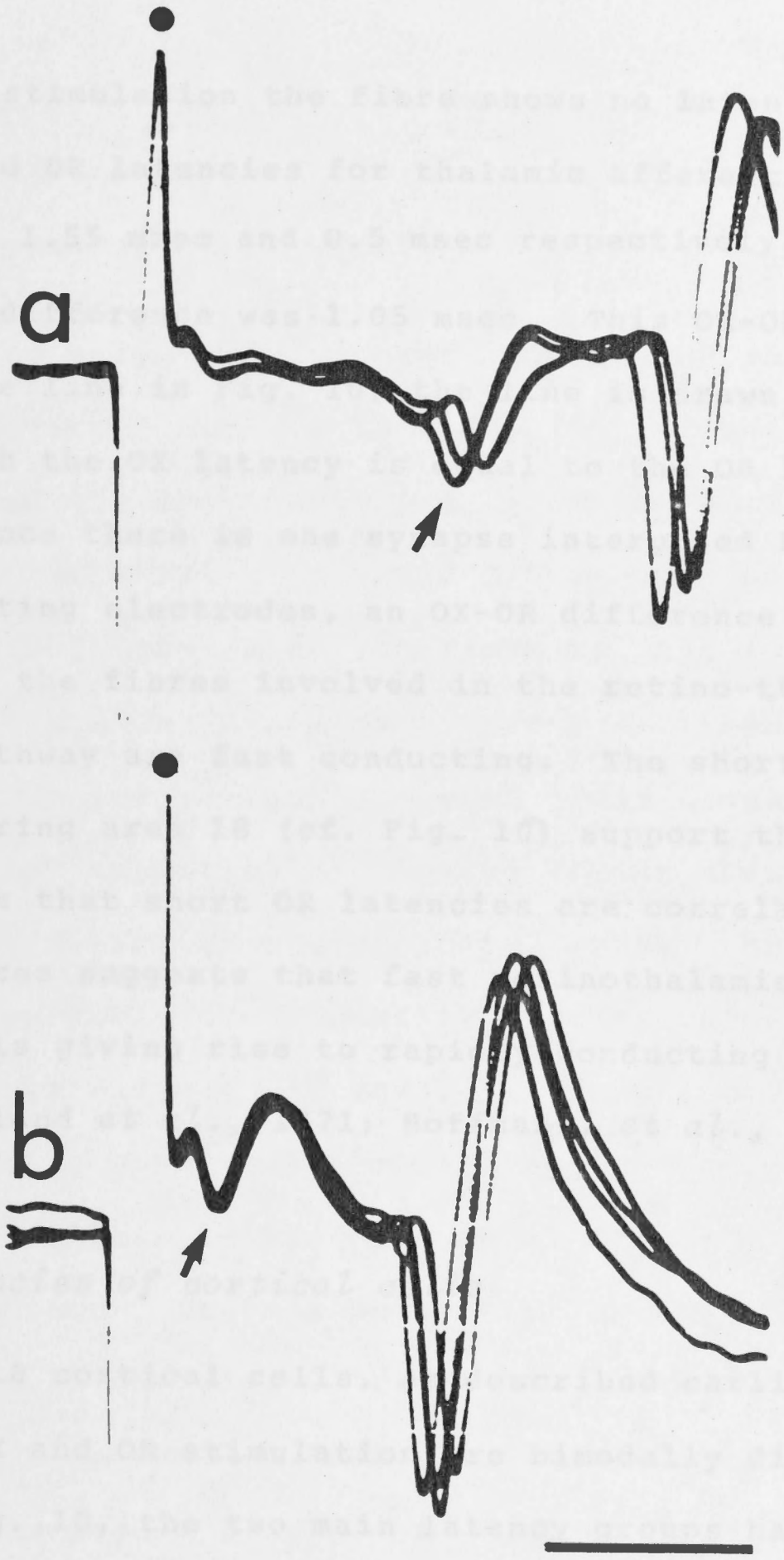


Fig. 11. Orthodromic activation of a geniculocortical fibre (arrowed) and a group 1 neuron recorded in area 18. a, optic chiasm stimulation; b, optic radiation stimulation. Marker indicates 1 msec.

that after OR stimulation the fibre shows no latency variation. The mean OX and OR latencies for thalamic afferents recorded in area 18 was 1.55 msec and 0.5 msec respectively. Thus the mean OX-OR latency difference was 1.05 msec. This OX-OR difference is shown as the line in Fig. 10; 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-thalamo-parastriate pathway are fast conducting. The short OR latencies of fibres entering area 18 (cf. Fig. 10) support this proposition. The observation that short OR latencies are correlated with small OX-OR differences suggests that fast retinothalamic fibres synapse on cells giving rise to rapidly conducting geniculocortical axons (cf. Cleland *et al.*, 1971; Hoffmann, *et al.*, 1972; Cleland *et al.*, 1976).

OX and OR latencies of cortical cells

For area 18 cortical cells, as described earlier, the latencies to OX and OR stimulation are bimodally distributed. As shown in Fig. 10, the two main latency groups have been labelled group 1 and group 2. All 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. Group 2 neurons have been defined as having OX latencies between 3.0 and 4.0 msec and OR latencies between 2.0 and 3.0 msec. Twenty-one cells have OX and OR latencies which do not fall within groups 1 and 2 as defined above. These remaining cells have been placed in a separate category and defined as group 3 neurons. An example of a group 1 neuron excited from OX and OR

is presented in Fig. 11. The minimum OX and OR latencies of this cell were 2.4 msec and 1.25 msec respectively. The latency variation is characteristic of orthodromic, postsynaptic responses.

Considering only the first two groups, the mean OX and OR latencies for group 1 neurons (N = 78) is 2.4 and 1.3 msec respectively and the mean latencies to OX and OR stimulation for group 2 neurons (N = 52) is 3.6 and 2.5 msec. The OX-OR latency difference for both groups is therefore 1.1 msec; thus although the *absolute* OX and OR latencies of group 2 neurons 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 afferent geniculocortical axons. Since the mean OX-OR difference for geniculocortical fibres is almost identical to the mean OX-OR differences for both group 1 and group 2 neurons, it can be concluded that the axons recorded presynaptically in area 18 belong to the same population as those innervating parastriate neurons. 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 geniculocortical fibres (Fig. 10). This result provides further indication that the difference in latencies between group 1 and group 2 neurons is not due to variation in the conduction velocity of afferent fibres. The observed latency differences must therefore be *cortical* in origin.

The average OR latency difference between geniculate fibres and group 1 neurons is 0.8 msec and between group 1 and group 2 neurons is 1.2 msec. The latency difference (0.8 msec) between the afferent axons and the postsynaptic group 1 cells

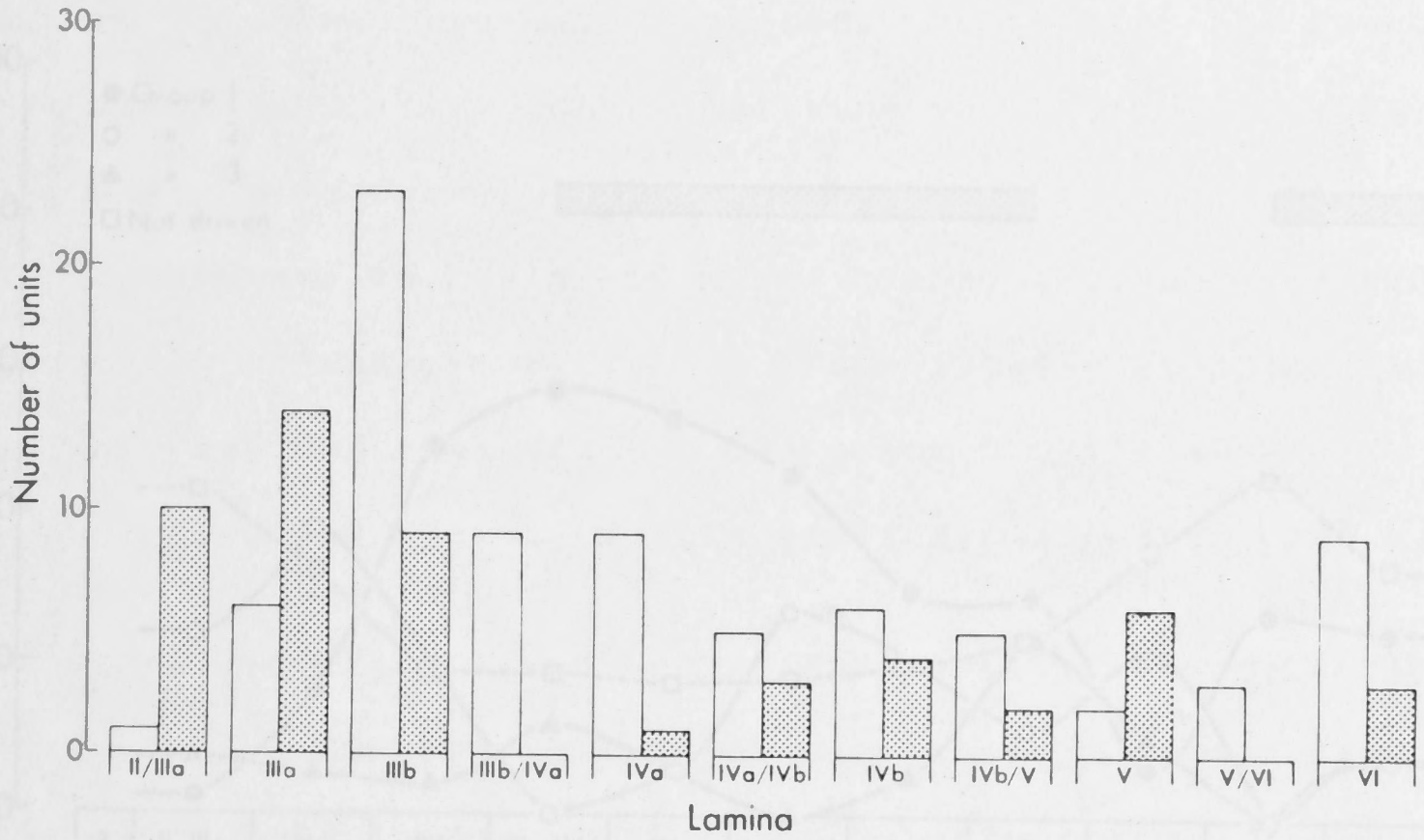


Fig. 12. The number of group 1 and group 2 neurons recorded in each cortical lamina of area 18. Dotted blocks, group 2; open blocks, group 1.

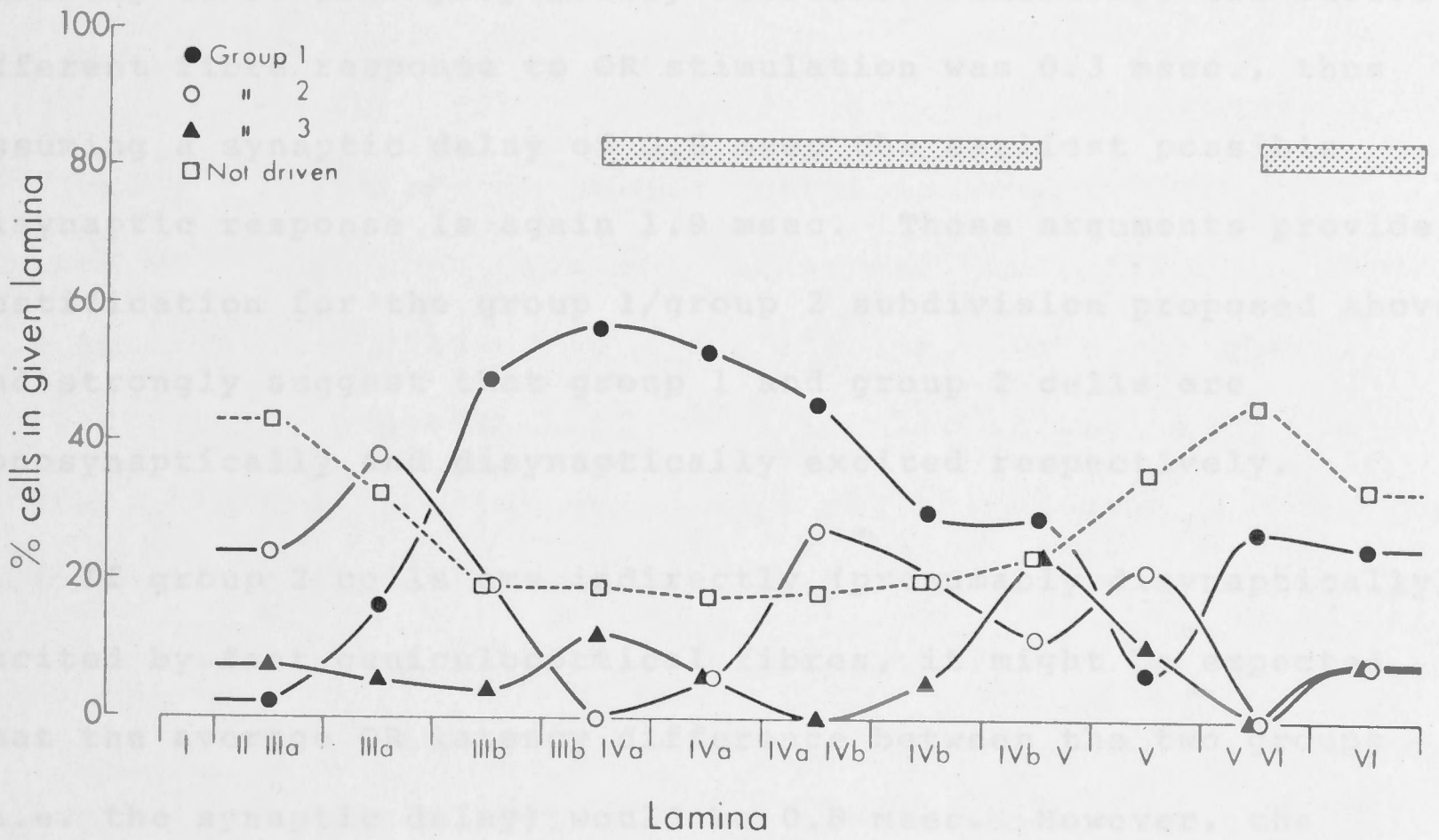


Fig. 13. The relative proportions in each cortical lamina of group 1, group 2 and group 3 neurons and cells that were not driven by electrical stimulation. Dotted bars, anatomically defined termination of geniculocortical fibres.

presumably represents the average synaptic transmission delay. The longest OR latency for a geniculocortical 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 synaptic delay of 0.8 msec the earliest possible disynaptic response is again 1.9 msec. These arguments provide justification for the group 1/group 2 subdivision proposed above and strongly suggest that group 1 and group 2 cells are monosynaptically and disynaptically excited respectively.

If group 2 cells are indirectly (presumably disynaptically) excited by fast geniculocortical fibres, it might be expected that the average OR latency difference between the two groups (i.e. the synaptic delay) would be 0.8 msec. However, the observed latency difference is in fact 1.2 msec. The additional delay (0.4 msec) is likely to result from 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

Figure 12 shows the absolute number of group 1 and group 2 neurons recorded in the various laminae of area 18. This histogram is somewhat misleading however, in that it does not take into account the effects of uneven sampling in different cortical layers. In Fig. 13, the relative proportions of group 1, group 2 and group 3 units and cells that could not be driven by electrical stimulation are shown for each 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 (N) of cells tested by electrical stimulation in that lamina. The dotted bars indicate the anatomically defined termination of geniculocortical fibres in area 18 (cf. METHODS).

Group 1 cells are found most often in laminae IIIb, IVa, IVb and VI; up to about 50% of all neurons 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 neurons closely follows the anatomically defined laminar distribution of afferent terminals and is consistent with the suggestion that group 1 neurons are directly activated by geniculocortical fibres. Group 2 neurons predominate in layers II-IIIa, IIIa and V (shown anatomically to receive very few thalamic axons) and are very rare in lamina IIIb and IVa. These observations lend support to the suggestion that group 2 neurons are indirectly activated from the optic radiation. Units not excited by either OX or OR stimulation were chiefly located in laminae II-IIIa, IIIa, V and VI.

There is a peak in the distribution of group 3 cells close to lamina V. Many of these cells have long OX and OR latencies indicative of indirect activation from the thalamus. If these cells are considered along with group 2 neurons then over 30% of all units encountered at the IVb/V border and in layer V itself are indirectly driven from OR. Cells driven only from OR (not shown in Fig. 13) 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 is shown in Table 3. The majority (53%) of S cells are group 1 neurons while only 10% of all S cells have latencies indicative 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. Similarly, there is almost no difference in the connectivity of S cells which contain either one or more stationary flashing light regions. There is no indication that group 2 S cells have larger receptive fields than group 1 cells.

Only 18% of C cells have OX and OR latencies indicative of a direct thalamocortical input; most C cells (49%) are group 2 neurons. Many of the group 3 C cells have OX and OR latencies greater than 4.0 and 3.0 msec respectively. If these cells are considered along with group 2 neurons, then 62% of all C cells are indirectly driven from the optic radiation. In all, 95% of parastriate C cells were activated after OX and/or OR stimulation. When compared with the overall C population, C cells which show little or no length summation more often have group 2 latencies. As with S cells, the receptive fields

TABLE 3

The afferent connectivity of parastriate receptive field classes

	LATENCY GROUP						
RECEPTIVE FIELD CLASS	1	2	3	OR only	OX only	NES	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
NVC	16	12	6	28	2	62	126

NES: Not driven by electrical stimulation

NVC: Not visually classified

N.O.: Non-oriented

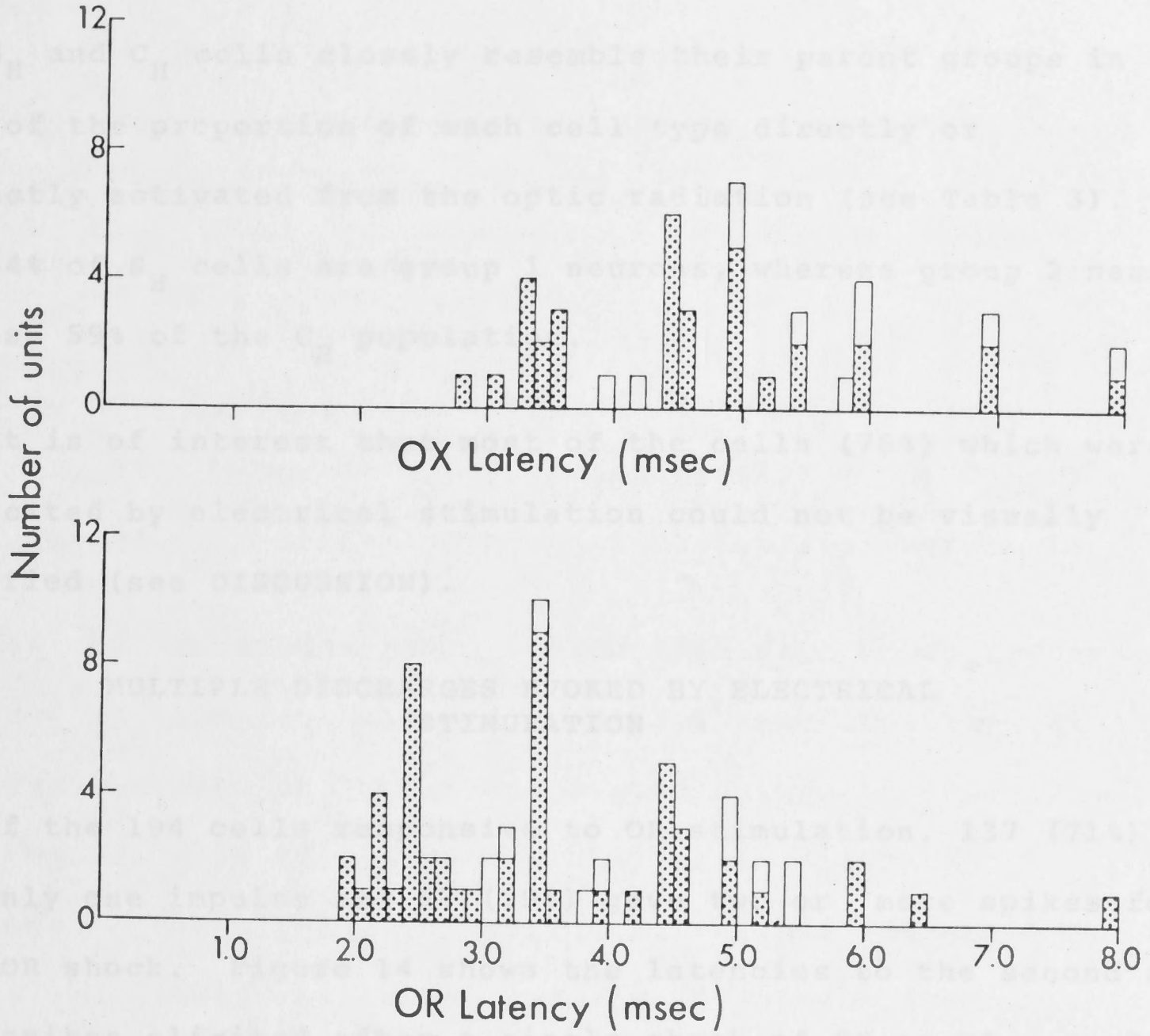


Fig. 14. Orthodromic latencies of the second and third spikes elicited after a single shock of the optic chiasm or optic radiation. Dotted blocks, second spike latencies; open blocks, third spike latencies.

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 directly or indirectly activated from the optic radiation (see Table 3). Thus 64% of S_H cells are group 1 neurons, whereas group 2 neurons comprise 59% of the C_H population.

It is of interest that most of the cells (76%) which were not excited by electrical stimulation could not be visually classified (see DISCUSSION).

MULTIPLE DISCHARGES EVOKED BY ELECTRICAL STIMULATION

Of the 194 cells responsive to OR stimulation, 137 (71%) gave only one impulse and 57 (29%) gave two or more spikes for every OR shock. Figure 14 shows the latencies to the second and third spikes elicited after a single shock of OX or OR. In 26 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 geniculocortical fibres and the first spikes of group 1 and group 2 neurons (cf. Fig. 10). Thus the longer OX and OR latencies of second spikes (Fig. 14) are not related to the speed of conduction of afferent axons and must 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 are mediated by polysynaptic pathways.

Considering only OR stimulation, 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 neurons and their second spike latencies are identical to the latencies of the *first* spike of group 2 neurons (mean OR latency = 2.4 msec). Thus the coincidence of group 1 second spike latencies and group 2 first spike latencies supports the proposition that group 2 neurons are disynaptically activated by geniculocortical afferents.

Most of the second spikes associated with group 2 neurons are found to have latencies of about 3.5 msec thus the latency difference between the first and second spikes of group 2 cells is 1.1 msec. This delay is very similar to the latency difference between the first spikes of group 1 and group 2 neurons and between the first and second spikes of group 1 neurons. It is probable therefore that these later group 2 afferent spikes are mediated via three synapses.

Tretter *et al.* (1975) have reported that C cells tend to fire repetitively after a single OR shock. Results from the present analysis are given in Table 4 which shows the relation between receptive field type and whether a cell produces single or multiple discharges after OR stimulation. Most (83%) S cells give only one spike per shock wereas C cells (73%) tend to give multiple discharges. Note also the S_H and C_H cells are similar in this regard to their parent cell groups.

TABLE 4

Multiple discharges evoked by electrical stimulation related to receptive field class

	RECEPTIVE FIELD CLASS								
	S	S_H	C	C_H	B	B_H	A	N.O.	NVC
1 spike	53	7	10	6	5	1	1	1	53
> 1 spike	11	2	27	5	1	1	0	1	9

N.O.: Non-oriented

NVC : Not visually classified

Concomitant with the finding that C cells comonly fire repetitively after OR stimulation, cells further away from the afferent input receive multiple inputs more often than cells directly driven by thalamocortical fibres. Only 26% of group 1 cells give more than one spike, compared with 44% of group 2 cells and 57% of group 3 cells. Lastly, there is no indication from the present results that S cells with multiple synaptic inputs (i.e. giving two or more spikes per OR shock) have larger receptive fields than S cells which apparently receive only one type of afferent input. A similar result is obtained for C cells.

DISCUSSION

Visual properties of area 18 neurons

S cells

S cells in the parastriate cortex have the smallest receptive fields, have a low spontaneous discharge and are sharply tuned for stimulus orientation. The majority show some preference for the direction of stimulus movement. Qualitative analysis indicates that many S cells in area 18 have monocular receptive fields but it is not clear whether these cells, like their counterparts in area 17, have subliminal excitatory or inhibitory areas in the non-dominant eye (Bishop, Henry and Smith, 1971). Such regions are difficult to locate using qualitative methods and quantitative experiments involving simultaneous binocular stimulation of the two eyes are necessary to show whether these subliminal areas exist. In addition, S cells in the striate cortex are extremely sensitive to the spatial disparity of binocularly presented visual stimuli (Nelson, Kato and Bishop, 1977). It is not yet known whether this is also a characteristic property of parastriate S cells.

In area 18, S cells are found throughout all layers of the cortex, but they are most common in laminae IIIb, IVa and VI. Their distribution is therefore very similar to the disposition of thalamocortical afferents, shown anatomically to terminate in layers IV and VI (see METHODS: Garey and Powell, 1971; Rosenquist, *et al.*, 1974; LeVay and Gilbert, 1976).

S cells are the most commonly encountered receptive field type in area 18 of the cat, comprising 53% of the total number

of visually classified cells in the present study. Tretter *et al.* (1975), Dreher and Cottee (1975) and Orban and Callens (1977a) have obtained similar results. Cells having receptive fields with only one ON or OFF area, or with spatially separate ON and OFF areas (all classed as S in the present study) made up 64% of the total sample of Tretter *et al.* (1975) and 40% of Dreher and Cottee's (1975) population, while Orban and Callens (1977a) reported that 50% of their visually classified cells had simple receptive field properties. Yamane, Nikara and Sugie (1977) have also described simple cells in area 18 though they found that these cells comprised only 31% of the total population.

The results presented above stand in direct contrast to those of Hubel and Wiesel (1965), who found no evidence for the existence of simple cells in area 18. Simple cells, as originally defined by Hubel and Wiesel (1962), can be subdivided into separate ON and OFF areas when tested with stationary flashing stimuli. The critical features that characterise simple cells are that they show summation within an ON or an OFF area as well as antagonism between neighbouring ON and OFF areas when both regions are stimulated simultaneously. Both simple and complex cells show summation as the *length* of a stimulus is increased along the line of optimal orientation. However, only simple cells summate when the *width* of a stationary flashing stimulus is increased in a direction perpendicular to the preferred orientation.

The classification scheme used in the present study does not lay any emphasis on the presence or absence of summation (cf. Henry, 1977) and it is therefore difficult to make a direct

comparison between the present results and those of Hubel and Wiesel. However, recent quantitative analysis of S cells in area 18 (Camarda, in preparation) indicates that many of these cells do show summation and antagonism characteristic of area 17 simple cells. S cells as described in this chapter would undoubtedly be classified as simple if the criteria of Bishop and Henry (1972) and Kato *et al.* (1978) are adopted. Indeed, the laminar distribution, afferent and efferent connections and overall receptive field properties of parastriate S cells are almost identical to their counterparts in the striate cortex. Thus irrespective of whether S cells in area 18 are really simple cells as defined by Hubel and Wiesel (1962), they appear to subserve a role in visual processing which is similar to the equivalent cells in area 17.

C and B cells

The present study has shown that C cells generally have the largest fields in the parastriate cortex and that there is a marked tendency for peripheral fields to be larger than those in the central visual representation. C cells generally have a relatively high rate of spontaneous discharge and the majority have binocular receptive fields (cf. Fig. 4). Summation along the length of the stimulus varies from one C cell to another. Cells which show rapid summation and are thus activated equally well by both short and extended targets are more direction selective than units which only respond to long stimuli. In terms of the proportion of cells encountered in any given lamina, C cells are most commonly encountered in layers IVb and V.

Neurons classified as C cells made up 26% of the total population of visually classified cells in area 18. In comparison, Tretter *et al.*(1975) reported that 27% of their sample were group 3 cells (which are equivalent to the C cell as described in the present study), Dreher and Cottee (1975) found that 33% of their area 18 cells were C type, while Orban and Callens (1977a)found that complex cells constituted 18% of their population. These figures are much lower than those of Hubel and Wiesel (1965),who claimed that 96% of cells recorded in area 18 had complex receptive fields. This discrepancy in the C cell populations, when considered along with the already described difference in the encounter rates of S cells,indicates that many of Hubel and Wiesel's complex cells have been classed as S, or simple, by other workers.

B cells are apparently not common in area 18. In area 17, B cells make up the greater part of the projection to the Clare-Bishop cortex (Henry, Lund and Harvey, 1978). Area 18 also sends axons to this association area but the receptive field classes which contribute to this pathway are not yet known. If parastriate B cells are efferent to the Clare-Bishop area, it would add weight to the suggestion that these cells constitute a distinct receptive field class which is equivalent to the B cell group of area 17.

The H property

Cells which possess end-zone inhibition and thus respond optimally to stimuli of restricted length are found most commonly in the superficial layers of area 18. All three major

cell groups (S, C and B) can have hypercomplex or H properties, a result similar to that found in area 17 (Dreher, 1972; Camarda and Rizzolatti,1976a; Wilson and Sherman, 1976; Rose, 1977; Henry *et al.*, 1978; Kato *et al.*, 1978).

The thalamic input to area 18

Geniculocortical fibres recorded in area 18

Geniculocortical fibres are commonly encountered in the middle to deep layers of the grey matter of cat area 18. As would be expected from previous anatomical and physiological studies (see INTRODUCTION), nearly all of the afferent fibres activated from both the optic chiasm and optic radiation have OX-OR latency differences indicative of fast axonal conduction. In addition, the size of the receptive fields and the responsiveness to fast stimulus velocities suggests that the majority of the geniculocortical axons recorded in area 18 are probably Y-type (Hoffmann *et al.*, 1972) or brisk transient (Cleland *et al.*, 1971). These results are in keeping with the proposition that area 18 is innervated mainly by axons arising from Y cells in the dLGN and in MIN. Significantly, the mean OX-OR latency difference for afferent fibres is identical to the mean OX-OR latency differences of both group 1 and group 2 cortical cell populations. The fibres recorded presynaptically in area 18 therefore belong to the same population as those innervating parastriate neurons.

The afferent connections of area 18 neurons

About 75% of the cortical neurons excited by stimulation of the primary visual pathway were activated from both OX and OR.

The OX-OR latency differences of both group 1 and group 2 cells are indicative of innervation by fast(presumably Y) geniculocortical fibres, even though the *absolute* OR and OX latencies of group 2 neurons are 1.0 to 1.5 msec longer than those in group 1. Consequently, the longer latencies of group 2 neurons are not related to the conduction velocity of incoming afferent fibres, but appear to arise from extra delays occurring within the cortex itself. From an examination of the range of OR latencies of geniculocortical fibres recorded in area 18, it is apparent that orthodromic postsynaptic responses of less than about 2.0 msec are unlikely to be mediated by more than one synapse, while latencies greater than 2.0 msec are too long to be consistent with direct excitation by thalamic afferents. The relatively short latency group 1 cells are regarded as being directly or monosynaptically excited by thalamic afferents, while the longer OX and OR latencies of group 2 neurons are indicative of indirect (presumably disynaptic) activation by geniculocortical fibres. The latencies of some group 3 neurons suggest that there are three synapses interposed between the presynaptic afferent terminals and these long latency cells.

Consistent with the proposition that group 1 cells are directly and group 2 cells are indirectly driven by primary afferents, group 1 cells are concentrated in the cortical layers shown anatomically to be the site of geniculocortical fibre termination, while group 2 cells are commonly found in non-receiving laminae (Fig. 13). In addition, the minimum latencies of group 2 neurons are similar to the second spike latencies of group 1 cells. Since repetitive firing of cortical cells after a single OR shock is consistent with multiple synaptic inputs

(Tretter *et al.*, 1975) this result can be taken as further evidence that the input to group 2 neurons is disynaptically mediated.

Forty-three cells could be excited by OR but not by OX stimulation. Some of the OR latencies were very short, suggestive of a fast input to these particular area 18 neurons. The OR latencies of 24 cells however, were longer than 2.0 msec. These long latencies could indicate either that long polysynaptic pathways are involved or that the afferent fibres mediating these orthodromic responses are slow conducting. No slowly conducting fibres were 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 and are not responsive to visual stimuli (Table 3) is perhaps indicative of polysynaptic input. However, it should be stressed that the possibility that some slowly conducting axons project to area 18 cannot be ruled out.

Eighty-two (29%) of the area 18 units in the present sample were not activated from either stimulating site. These electrically non-drivable cells are found most commonly in the superficial and deep layers of the cortex and the greater proportion of these cells (76%) are also difficult to excite with visual stimuli. It is possible that these non-responsive neurons have been 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 to these cells is mediated by a large number of intracortical

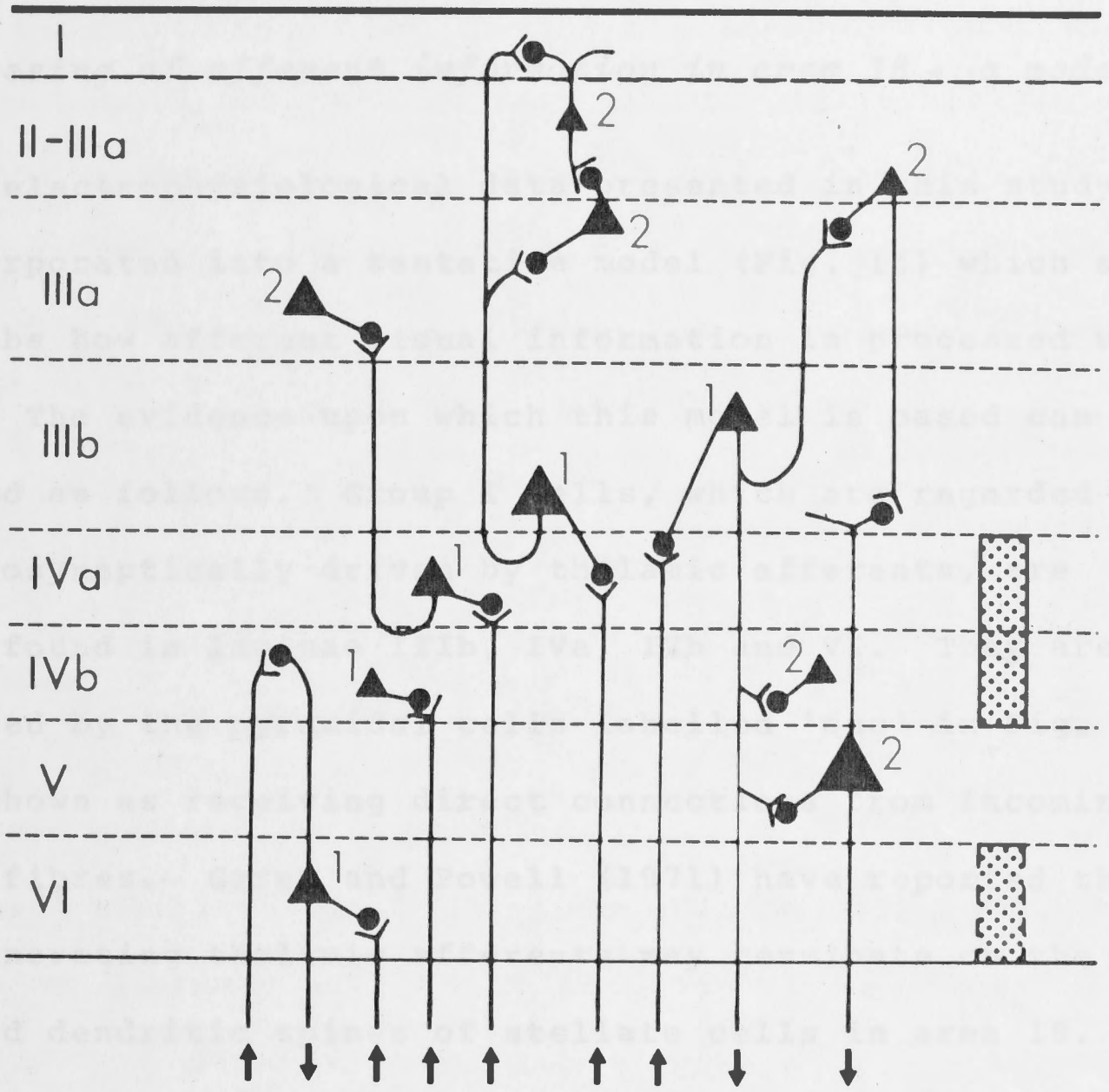


Fig. 15. A tentative model which depicts how incoming visual information is processed within area 18. The experimental basis for this model, as well as some of its implications are discussed in detail in the text. Cells labelled 1 and 2 represent group 1 and group 2 neurons respectively. Dotted bars on the right show the anatomically defined distribution of geniculocortical terminals.

synapses and that very specific visual stimuli are required to trigger these neurons.

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. 15) which attempts to describe how afferent visual information is processed within area 18. The evidence upon which this model is based can be summarised as follows. Group 1 cells, which are regarded as being monosynaptically driven by thalamic afferents, are commonly found in laminae IIIb, IVa, IVb and VI. They are represented by the pyramidal cells labelled 'one' in Fig. 15 and are shown as receiving direct connections from incoming thalamic fibres. Garey and Powell (1971) have reported that some degenerating thalamic afferents may terminate on the cell bodies and dendritic spines of stellate cells in area 18. Golgi studies indicate that stellate cells with spine-laden dendritic processes are common in lamina IV of area 17 in both cat and monkey (Lund, Henry, Macqueen and Harvey, in preparation; Lund, 1973) however similar studies in cat area 18 have not yet been undertaken and it is not yet clear whether layer IV spiny stellate cells also occur in this cortical region. Thus although Fig. 15 shows all cells as having pyramidal morphology, it should be pointed out that some neurons, especially those in lamina IV, may in fact have stellate morphology.

Group 1 cells in layers IV and VI occur in the laminae which anatomically have been shown to receive thalamocortical fibres (shown as the dotted bars in Fig. 15). Lamina VI neurons are

shown as being directly excited in two different ways; one via a thalamic terminal and an apical dendrite in 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. As shown in Fig. 15 it is proposed that these cells in deep III have pyramidal morphology and have basal dendrites which reach down into layer IVa and perhaps IVb. Such cells would therefore have access to incoming afferent information. Group 1 cells are also shown as having only a single major excitatory input, since group 1 neurons rarely produce multiple spikes after single shocks of the optic radiation.

Group 2 neurons (which are suggested as being disynaptically activated by thalamic afferents) are commonly encountered in laminae II-IIIa, IIIa and V. In consequence, group 2 neurons in these layers are shown (Fig. 15) as receiving excitatory inputs from group 1 cells. Since cells in the middle to superficial parts of lamina III are often only indirectly driven from the thalamus, the basal dendrites of these pyramidal neurons are unlikely to extend down into layer IVa. It is suggested that these group 2 cells are innervated by the recurrent axons of group 1 neurons. Although the large pyramids in layer V have apical dendrites which pass up through layer IV, the fact that the majority of layer V neurons are indirectly activated from the thalamus suggests that these dendrites are not contacted by afferent terminals. In the monkey striate cortex, it has been shown that the apical dendrites of layer V pyramidal cells lose their spines in the laminae in which

geniculocortical fibres terminate (Lund and Boothe, 1975). Since most thalamic afferents synapse on dendritic spines (Garey and Powell, 1971), it can be inferred that these layer V neurons are not innervated by afferent nerve endings. It would be of interest to know if a similar pattern is also present in area 18 of the cat.

Indirectly driven area 18 neurons often fire repetitively after a single optic radiation shock which indicates that there are multiple synaptic inputs onto these cells (cf. Tretter *et al.*, 1975). One lamina III cell and one neuron 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 evidence for these projections is described elsewhere (Chapters 3, 4 and 5) but it is worth mentioning at this point that layer VI corticothalamic cells are commonly monosynaptically excited by thalamic afferents, while layer V corticocollicular neurons are generally indirectly activated by thalamic fibres. Many of the cortico-cortical cells in layer IIIb are also innervated directly by ascending geniculocortical afferents.

In terms of its afferent connectivity, layer IVb appears to be intermediate between laminae IIIb-IVa and lamina V. In Fig. 15, one cell in layer IVb is shown as being disynaptically activated by incoming thalamic fibres. However, it is possible that some of the units thought to be in lamina IVb actually

have their somata in layer V since one cannot be certain, using extracellular recording techniques, that the electrode is necessarily positioned close to the cell body. In Chapter 3, it is shown that corticocollicular units (which have fast conducting axons and therefore presumably large cell somata) are occasionally recorded in laminae IV and VI even though anatomical evidence suggests that the projection to the superior colliculus arises solely from cells in lamina V. It would seem therefore that the responses recorded in layers other than lamina V must be of dendritic or axonic origin. On the other hand the smaller cells which project to the dLGN are never recorded outside lamina VI, the layer shown anatomically to project to this subcortical site. These results suggest that the larger the cell, the greater the possibility of recording at sites well away from the cell body. Since layer V pyramids are among the largest in area 18, it is quite possible that some of the group 2 units apparently located in layer IVb might in fact be in lamina V, the recording being made from the apical dendrites or recurrent axons, rather than from the cell somata themselves. Generally, however, the good correlation between the disposition of the electrophysiologically defined cell groups and the anatomical distribution of thalamic terminals suggests that recording distal to the cell body is rare and occurs only when the largest neurons in the cortex are involved.

The initial steps in the processing of afferent information in area 18 can now be summarised. Cells in laminae IIIb, IVa, IVb and VI are driven monosynaptically by incoming geniculo-cortical fibres. Some of these group 1 neurons in layers IIIb

and VI send axons out of the cortex, but the majority appear to pass their information onto second order cortical cells. These group 2 neurons are commonly found in laminae III and V. At this stage, some layer V cells project subcortically, however there are indications that many group 2 cells are involved in further intracortical processing within laminae II-IIIa, IIIa and perhaps also lamina VI. It should 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 model described in the previous section has been based on the experimental data obtained from electrical stimulation of the primary visual pathway. As well as determining their afferent connectivity, the receptive fields of many area 18 cells were also characterised. It is therefore possible to relate the excitatory intracortical circuits shown in Fig. 15 with the visual properties of parastriate neurons.

Of the S cells tested by electrical stimulation, 84% could be activated from either the optic chiasm or optic radiation. Fifty-four cells were excited from both stimulating sites and 43 of these cells had latencies suggestive of monosynaptic innervation by geniculocortical fibres. It is therefore apparent

that S cells in area 18 are commonly first order neurons, receiving their input directly from primary afferents.

In comparison, 95% of all C cells recorded in the present study were driven from at least one of the two stimulating sites. Only 18% of these electrically excitable C cells had OX-OR latencies indicative of monosynaptic excitation by geniculo-cortical fibres, while 62% had latencies consistent with indirect activation by primary afferents. It would seem then, that C cells are rarely first order neurons, but commonly receive their excitatory input from other cortical cells. Specifically, 19 of the 34 C cells excited from both stimulating sites had latencies which indicated that they were disynaptically activated by thalamic axons. Of the small number of parastriate B cells in the present sample, the majority appear to resemble C cells in their afferent connectivity.

In Fig. 15, group 1 neurons are shown to predominate in laminae IIIb, IVa and VI, while group 2 neurons occur more commonly in layers II, upper III and V. The majority of these group 1 neurons are likely to be S cells whereas many group 2 cells will probably have C type receptive fields. Consistent with this proposition, (which has been shown directly using both visual and electrical stimulation) S cells occur most frequently in laminae IIIb, IVa and VI, while C cells are commonly encountered in laminae IVb and V.

Although most S cells are group 1 neurons, an occasional cell was encountered which was indirectly excited by thalamic axons. Such cells were always located in laminae which do not receive afferent fibres. In contrast, the relatively small

number of C cells with group 1 latencies were always found to be in a zone between laminae IIIb and IVb. This observation indicates that the laminar position of a cell is an important factor in determining its afferent connectivity. However, group 1 S cells were found in non-receiving layers, while C cells with group 2 latencies were sometimes located within the thalamic receiving zones. This suggests that although laminar position is of importance, there may be an overriding predisposition for S cells, wherever they are, to be directly excited, while C cells are generally indirectly activated by geniculocortical afferents.

This result is of interest in light of the hierarchical model of visual processing first suggested by Hubel and Wiesel (1962, 1965). From an examination of the receptive field properties and laminar distribution of visual cortical cells, Hubel and Wiesel proposed that simple cells in the striate cortex were first order neurons, receiving their input directly from geniculate fibres. Complex cells in area 17 and 18 were regarded as second order and their receptive fields were thought to be derived from the excitatory convergence of a small number of lower order simple cells. Finally, their scheme proposed that complex cells provided the input to the hypercomplex cells of areas 18 and 19.

The present results indicate that many S cells in the parastriate cortex are first order (i.e. group 1) and that a significant number of C cells are second order (group 2) neurons. Although it is not possible to identify the cortical neurons which are afferent to parastriate C cells, the small number of group 1 C cells appears to be insufficient to account for all

of the input to C cells with group 2 and group 3 latencies. Since most monosynaptically driven cells in area 18 have S properties and since the number of group 2 S cells is small, it is possible that many of these group 1 S neurons are providing the input to higher order C cells. This suggestion is consistent with the hierarchical model of Hubel and Wiesel (1962, 1965),although it should be stressed that they considered area 17 and not area 18 simple cells (which they claimed did not exist) to be afferent to parastriate complex neurons.

After a single shock of the optic radiation, S cells in area 18 generally respond only once whereas the majority of C cells fire repetitively. Unlike S cells therefore, C cells commonly receive multiple synaptic inputs (Tretter *et al.*, 1975) and there is thus a high degree of excitatory convergence onto these neurons. This result might be expected if a number of S cells provide the input to a C cell. However, the above response properties of S and C cells are also characteristic of group 2 S and group 1 C cells, which suggests that the degree of excitatory convergence may be related to the receptive field type rather than to the position of the cell in the afferent processing chain.

Although much of the analysis so far is consistent with a hierarchical scheme, there are a number of observations which suggest that the situation is more complicated. Firstly, there are a few S cells with group 2 latencies and a small number of C cells which are monosynaptically excited by thalamic afferents. Furthermore, there are no discernible differences in the receptive field properties of group 1 and group 2 S cells or group 1 and

group 2 C cells. These results are difficult to interpret in the context of a simple hierarchical model of visual processing.

In addition, Hubel and Wiesel (1965)proposed that hypercomplex or H cells were third order neurons. However, it is clear from the present work that many H cells (especially S_H neurons) are directly driven by thalamic afferents. In terms of the afferent connections of H cells in area 18, S_H cells resemble S cells in that the majority are monosynaptically innervated by fast conducting geniculocortical fibres. Most C_H cells, on the other hand, are indirectly activated by large thalamic afferents and these cells therefore resemble C cells in their connectivity.

The similarity in the afferent connections of S_H and S cells and C_H and C cells suggests that the 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 predominently determined by their afferent excitatory connections. 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. However, end-zone inhibition could 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 dLGN neurons (Levick, Cleland and Dubin, 1972; Dreher and Sanderson, 1973).

Irrespective of the mechamisms which produce end-zone inhibition, it would seem at least in area 18, that this receptive field property is not related to the position of the cell within the excitatory cortical processing chain.

Interaction between areas 17 and 18

As well as proposing how afferent signals were elaborated within the stiate cortex, Hubel and Wiesel (1965) also used their heirarchical model to explain how visual information is transferred from one visual area to another. They believed that area 17 was unique in being the site of geniculocortical fibre termination and that areas 18 and 19 were serially related visual areas receiving their input via area 17. In support of this, Hubel and Wiesel (1962, 1965) presented evidence which showed that simple cells were most common in area 17, complex cells in area 18, and hypercomplex cells in area 19.

Since this early report, it is now widely agreed that much of the processing of visual information which occurs in 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 responds independently of the more medial parts of the cortex. More recently, both Dreher and Cottee (1975) and Sherk (1978) have used single unit techniques to record from area 18 neurons before and after inactivation of area 17. The selectivity of parastriate cells for the orientation and direction of movement of a visual stimulus is not greatly altered by removal or cooling of area 17. There is a tendency for area 18 units to become less responsive

to slowly moving stimuli, however both reports conclude that area 18, to a large extent, processes afferent visual information in parallel to area 17. Anatomical studies, which have shown that area 18 of the cat receives a significant projection from the large cells of both the dLGN and MIN (see INTRODUCTION), provide the structural basis for the physiological findings described above.

The present study has shown that a substantial number of area 18 neurons are driven either directly or indirectly by fast conducting geniculocortical fibres. Of the units tested with electrical stimulation, 71% were orthodromically driven from either the optic chiasm or the optic radiation. In the laminae which receive thalamic afferents, the proportion of electrically excitable units is as high as 83%. These results indicate that much of the visual input to area 18 is directly mediated by thalamic afferents. The present analysis thus supports the contention that area 18 processes visual information largely in parallel to area 17, yet at the same time provides evidence that within area 18, a heirarchical organisation similar to that proposed by Hubel and Wiesel (1962, 1965)may indeed exist.

Although areas 17 and 18 appear to function independently of each other, anatomical studies indicate some degree of interaction between the two areas. Hubel and Wiesel (1965), Wilson (1968) and Kawamura (1973) have shown,using degeneration techniques, that area 17 projects onto area 18. Wilson (1968) and Kawamura (1973) have also reported that area 18 sends axons into area 17. On the other hand, the HRP studies of Gilbert and Kelly (1975) while confirming the projection from the striate

to the parastriate cortex, failed to find any evidence for an input to area 17 from area 18. If the two areas are indeed reciprocally connected, it would seem that each area is dependent, so some extent, on the activity of its neighbour. The experiments of Dreher and Cottee (1975) and Sherk (1978) do indicate some changes in the response properties of area 18 neurons after ablation or cooling of area 17, but the effects are not large.

The exact nature of the interaction between the two areas has yet to be elucidated. Some inferences can be drawn however, from experiments which have studied the callosal connections in areas 17 and 18 of the cat (Chapter 5). Efferent callosal units are heterogeneous in their receptive field properties and are commonly found in the deeper parts of layer III. Cells receiving commissural fibres are commonly C or B cells, are often located in the superficial laminae and are usually indirectly excited by primary afferents. These results suggest that corticocortical interactions may be most common between higher order neurons in the upper reaches of the cortex (cf. Tretter *et al.*, 1975). In the present study, many neurons in layers II-IIIa and IIIa of area 18 were not excited by either visual or electrical stimulation. It is possible that these cells are more dependent on the input from other cortical regions and hence are less easy to characterise. In this context, however, it is worth pointing out that most of the parastriate cells in Sherk's (1978) sample were recorded in layers II and III, yet were only marginally affected by inactivation of area 17.

The functional roles of areas 17 and 18

Although in general terms the intrinsic organization of areas 17 and 18 appears to be very similar (see below), significant differences are apparent which appear to be related to the type of afferent fibres innervating the two regions. Area 18 is predominently innervated by Y cells from the dLGN and MIN (see INTRODUCTION). In contrast, anatomical and physiological evidence suggests that many of the geniculocortical fibres entering area 17 are smaller in diameter, more slowly conducting and are derived from medium-sized neurons within the dLGN whose receptive field properties are typical of X cells (Garey and Powell, 1971; Stone and Dreher, 1973; Gilbert and Kelly, 1975; Singer *et al.*, 1975; Garey and Blakemore, 1977; Hollander and Vanegas, 1977; LeVay and Ferster, 1977). These papers also present evidence that some large Y-type dLGN neurons innervate the striate cortex. Physiologically, Singer *et al.* (1975) have reported that both simple and complex cells in area 17 can be excited by either X or Y thalamic afferents, whereas Stone and Dreher (1973) have claimed that simple cells are driven by X and complex cells by Y fibres. The results presented in Chapter 1, to some extent, support both suggestions in that S and C cells are occasionally excited by fast geniculate fibres whereas many S but no C cells are monosynaptically driven by slower conducting afferent fibres.

Despite the evidence for a fast input to area 17, this projection appears to be small when compared with the X cell projection to this area (Chapter 1; Garey and Blakemore, 1977; Hollander and Vanegas, 1977; LeVay and Ferster, 1977). Generally, therefore, it can be stated that area 17 is primarily innervated

by X and area 18 by Y thalamic afferents. This difference is reflected in the visual properties of cortical neurons in the two regions. Within any receptive field class, area 18 fields are always larger than their counterparts in are 17. In addition, cells in area 18 commonly responded to faster stimulus movements. Both of these differences are also apparent when the receptive field properties of X and Y cells are compared; cells with Y or brisk transient characteristics generally have larger receptive fields and respond to fast stimulus velocities (e.g. Hoffmann *et al.*, 1972).

It has been suggested that area 18, 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 (Tretter *et al.*, 1975; Orban, 1977). The suggestion is supported by the observation that there is a considerable expansion of the cortical representation of the area centralis in area 17, while area 18 in contrast, contains only a small area of cortex devoted to central processing. 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 similarities in the intrinsic organization and efferent projections of the two areas suggest another possibility. That is, *within each region*, S cells are involved in the processing of form vision while C cells are primarily concerned with the temporal aspects of perception.

Considering the S cell, they are most frequently encountered in laminae IV and VI in both areas 17 and 18. These are the laminae in which thalamic afferents terminate and the results presented in this chapter clearly show that the majority of S cells in area 18 are innervated directly by incoming primary fibres. The data are less complete in area 17, but there are indications that S cells are commonly excited directly by thalamic afferents. In both areas, the proportion of S cells with monocular receptive fields is the highest of any cell type in the cortex. S cells in both striate and parastriate visual areas have the smallest receptive fields, the slowest optimal stimulus velocity, the sharpest orientation tuning and generally have no or only rare spontaneous activity. Lastly, the slow conducting efferent projection from lamina VI to the dLGN consists of S cells in both areas 17 and 18 (Chapter 3).

C cells in areas 17 and 18 are most commonly located in and around lamina V. In area 18, the majority of C cells have group 2 latencies indicative of disynaptic activation by thalamic afferents. However, the data on area 17 is not detailed enough to allow comparison although there may be differences in the connectivity of striate C cells (Chapter 1; Stone and Dreher, 1973). The majority of C cells in both visual areas have binocular receptive fields. In addition they tend to have the largest receptive fields, repond to relatively fast stimulus velocities, are broadly tuned for orientation and almost always have a relatively high rate of spontaneous discharge. In terms of their afferent projections, layer V C cells in both the striate and parastriate cortex project to the superior colliculus (Chapter 3).

Lastly, as in the striate cortex, all receptive field types in area 18 can possess the property of end-zone inhibition. In both areas, H cells are most commonly encountered in the superficial layers of the cortex.

In many ways then, S cells in the striate and parastriate cortex appear to be more closely related to each other than S and C cells within either area 17 or area 18. Similarly, the receptive field properties and efferent projections of C cells in the two visual areas are, for the most part, identical. Of particular interest in this context are the sub-cortical projections of the two areas. The cortical projection to the dLGN is thought to be concerned with the binocular fixation of visual stimuli (Schmielau and Singer, 1977; Harvey,1978; Chapter 3) whereas the projection to the superior colliculus is believed to be involved in attention and the control of eye movements directed towards a novel stimulus (cf. Chapter 3). If areas 17 and 18 are concerned solely with form and motion perception respectively, it might be expected that the striate cortex would be efferent to the dLGN while the parastriate cortex would project to the superior colliculus. This is not the case, S cells in both cortical regions send axons to the dLGN whereas C cells in the two areas project to the superior colliculus.

Levick (1977) has suggested that the brisk transient system is involved in the binocular vision of objects close to the cat. This hypothesis is based on the nature of the crossed-uncrossed distribution of axons from brisk transient retinal ganglion cells. As he points out, stimuli moving closer to the animal

would have an increased angular size and greater angular velocity. The large receptive fields and responsiveness to fast movements characteristic of brisk transient units makes them ideally suited for encoding information about these objects.

It is clear from the receptive field properties of striate and parastriate neurons that both form and motion can be recognised in the two regions. Cells in the striate cortex are best activated by relatively small, slowly moving targets while parastriate neurons respond to larger, fast moving stimuli. It is tempting to suggest that area 17 is concerned in the perception of objects distant from the animal whereas area 18 is primarily concerned with the analysis of stimuli more proximal to the cat. If this is the case, it might be expected that binocular neurons in area 18 would have systematically greater crossed disparities than cells in area 17. This was not evident in the present study, but further work is necessary to check this possibility.

CHAPTER THREE

THE PROJECTIONS OF AREAS 17 AND 18 TO THE THALAMUS AND SUPERIOR COLLICULUS

INTRODUCTION

The previous two chapters have described the initial steps by which afferent visual information is processed within areas 17 and 18 of the cat cerebral cortex. We do not, as yet, possess a complete understanding of the intrinsic organisation of these occipital areas and it is therefore difficult to be certain about their role in visual perception per se. It is possible, however, to gain some insight into the functional importance of these visual areas by studying how their efferent projections interact with and influence the behaviour of subcortical structures.

Anatomically, areas 17 and 18 of the cat have been shown to project retinotopically to a number of sites in the thalamus and midbrain. In terms of the thalamic projection, degeneration and autoradiographic studies indicate that both cortical areas send axons to the dorsal lateral geniculate nucleus (Garey, Jones and Powell, 1968; Hollander, 1970; Niimi, Kawamura and Ishimaru, 1971; Hollander, 1972; Kawamura, Sprague and Niimi, 1974; Updyke, 1975, 1977), the perigeniculate nucleus (Kawamura *et al.*, 1974; Updyke, 1975, 1977), the lateral posterior nucleus (Garey *et al.*, 1968; Niimi *et al.*, 1971; Graybiel, 1972; Kawamura *et al.*, 1974; Updyke, 1977; Berson and Graybiel, 1978) and the ventral lateral geniculate nucleus (Niimi *et al.*, 1971; Kawamura *et al.*, 1974; Updyke, 1977). A projection from both areas to the medial interlaminar nucleus has also been described (Updyke, 1977), however Niimi *et al.* (1971) and Kawamura *et al.* (1974) found no evidence for a projection from area 17. Areas 17 and 18 are also efferent to a number of midbrain structures. Both regions project to the superior colliculus (Garey *et al.*, 1968;

Kawamura *et al.*, 1974; Updyke, 1977), the pretectum (Kawamura *et al.*, 1974; Updyke, 1977) and the pontine nuclei (Garey *et al.*, 1968; Brodal, 1972a,b; Sanides, Fries and Albus, 1978).

The lamina of origin of a number of these corticofugal projections from the cat striate and parastriate cortex has been studied using the retrograde transport of horseradish peroxidase (HRP). Cells in lamina VI of both visual areas project to the dorsal lateral geniculate nucleus (Gilbert and Kelly, 1975; Tombol, Hajdu and Somogyi, 1975), while cells in lamina V send axons to the superior colliculus (Hollander, 1974; Gilbert and Kelly, 1975; Magalhäes-Castro, Saraiva and Magalhäes-Castro, 1975; Baleydier, 1977) and to the pontine nuclei (Albus and Donate-Oliver, 1977). The majority of these subcortically projecting neurons in layers V and VI have pyramidal morphology. In the monkey, layer VB of area 17 also sends axons to the pulvinar complex (Lund, Lund, Hendrickson, Bunt and Fuchs, 1975). Unpublished observations in the cat (Lund, Henry, Macqueen and Harvey) suggest a similar disposition for cortical cells projecting to a region(perhaps the lateral posterior nucleus) medial to the dorsal lateral geniculate nucleus.

By studying the response properties of single neurons in structures such as the superior colliculus (SC) and lateral geniculate nucleus (dLGN), before and after inactivation of the visual cortex, it is possible to infer how the anatomically identified corticofugal systems influence the behaviour of these subcortical regions. For example, removal or cooling of the visual cortex has marked effects on the response properties of cells in the superficial laminae of the superior colliculus

(Wickelgren and Sterling, 1969; Rizzolati, Tradardi and Camarda, 1970; Rosenquist and Palmer, 1971; Mize and Murphy, 1976). These experiments show that the direction selectivity and binocular responsiveness of collicular neurons are largely dependent on their input from the visual cortex. The effects of cortical inactivation on the visual properties of cells in the dLGN are, however, more subtle (Kalil and Chase, 1971; Schmielau and Singer, 1977). From their results, Schmielau and Singer (1977) have suggested that corticogeniculate fibres are involved in the control of binocular interactions in the dLGN, the result being an improvement in the contrast between objects in, as opposed to away from, the fixation plane (cf. Singer, 1977).

The experiments described above therefore provide important clues concerning the nature of the interaction between the visual cortex and subcortical regions such as the dLGN and SC. If the influences ascribed to the corticofugal systems are correct, then the receptive field properties of cortical cells which project to these subcortical areas should contain the necessary visual information required to carry out their respective functional tasks. A number of physiological studies have described the receptive field properties of neurons in areas 17 and 18 which send axons to the thalamus and midbrain. The projection to the superior colliculus has been examined in area 17 (Palmer and Rosenquist, 1974; Singer, Tretter and Cynader, 1975) and in area 18 (Tretter, Cynader and Singer, 1975). Other reports have studied the receptive field properties of corticothalamic neurons in the striate (Singer *et al.*, 1975; Gilbert, 1977; Harvey, 1978) and parastriate (Tretter *et al.*, 1975) cortex.

The present work further examines and compares the receptive field properties of corticothalamic and corticocollicular cells in the striate and parastriate cortex of the cat. With regard to the projection to the SC, the results are in general agreement with those of Palmer and Rosenquist (1974), Singer *et al.* (1975) and Tretter *et al.* (1975). A possible subdivision in the lamina VI projection to the dLGN and perigeniculate nucleus is discussed and the receptive fields of these cells are compared with those which appear to send axons to other thalamic areas. In addition, the primary afferent input to striate and parastriate cortico-collicular and corticothalamic neurons is also examined. The analysis of the receptive field properties of corticofugal neurons is discussed with regard to the functional significance of the various subcortical projections.

METHODS

The general experimental techniques employed in the present study have been described in Chapter 1.

In a large number of cats, stimulating electrodes were placed in the optic radiation (OR) in order to study the afferent connectivity of cortical neurons (Chapters 1 and 2). A number of cells in both areas 17 and 18 were antidromically activated from the OR stimulating electrodes. These neurons are amongst those described in the first part of the results section.

In order to study the efferent projections of the striate and parastriate cortex in more detail, stimulating electrodes were also placed in or close to the dLGN and in the superior colliculus (21 cats). Four electrodes were placed in the ipsilateral SC; two electrodes were positioned at about AP+ 1.5, lateral 1.0 and 3.5 mm and two were placed at AP + 4, lateral 1.0 and 3.5 mm. The system was arranged such that current could be passed between both posterior or anterior pairs as well as between the posterio-lateral and anterio-medial pair of stimulating electrodes. In a number of animals, the SC electrodes were used in the recording mode and the background activity was monitored as the electrodes were lowered towards the colliculus. The depth of the electrodes was altered until the best visually evoked responses were obtained. Subsequent histological examination revealed that the stimulating electrodes were always in the superior colliculus, usually at a depth of a millimetre or so from the tectal surface.

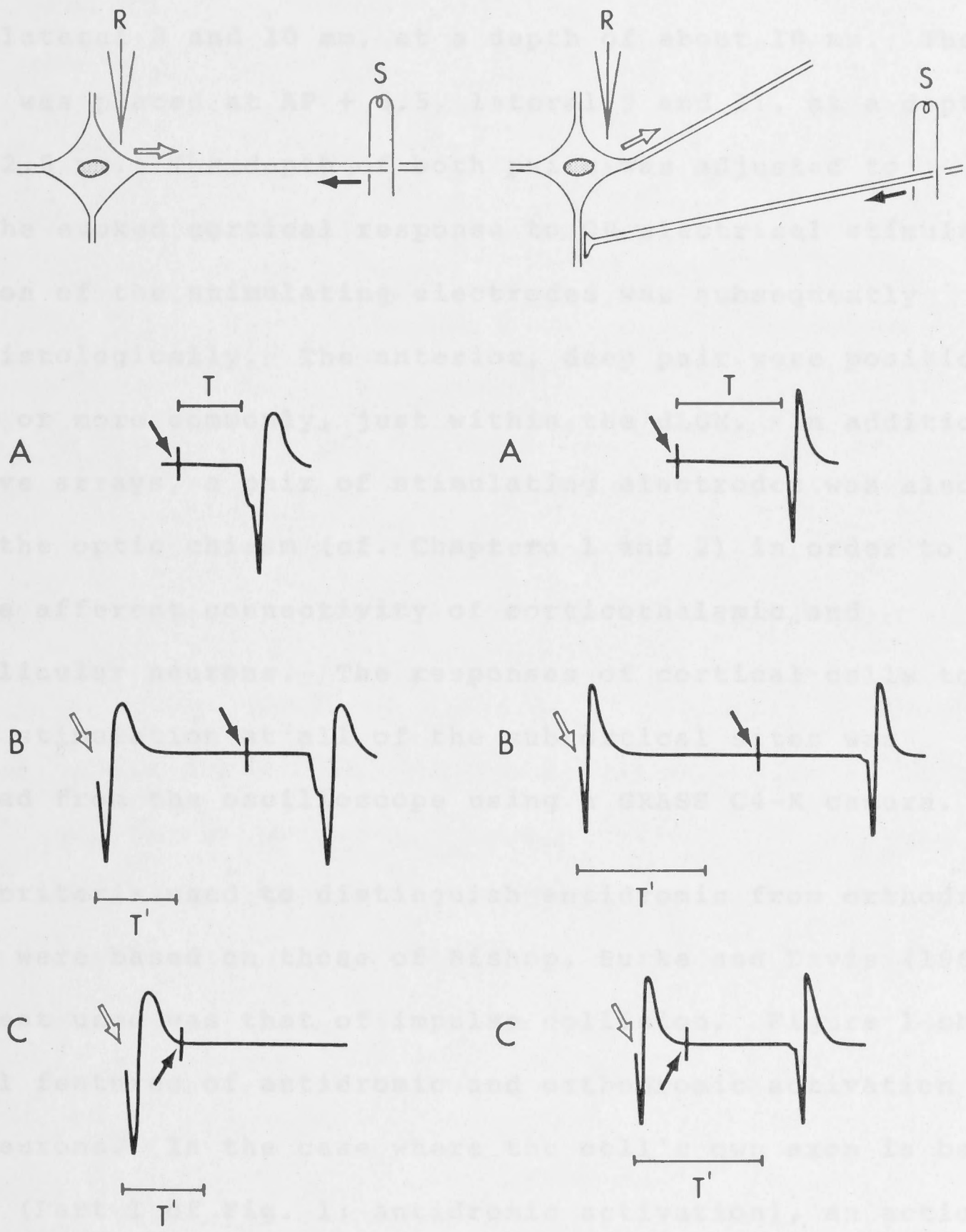


Fig. 1. Antidromic and orthodromic activation of a neuron. R, recording electrode; S, stimulating electrode. Open arrow, orthodromic action potential generated in cell body; filled arrow, impulse evoked by electrical stimulation. A-C: open arrows, as above; filled arrows, stimulus artifact. For further explanation - see text.

Four stimulating electrodes were also placed in the optic radiation. One pair was positioned at approximately AP + 5.5 to + 6.0, lateral 8 and 10 mm, at a depth of about 10 mm. The other pair was placed at AP + 6.5, lateral 9 and 11, at a depth of about 12.5 mm. The depth of both pairs was adjusted to maximise the evoked cortical response to OR electrical stimulation. The position of the stimulating electrodes was subsequently verified histologically. The anterior, deep pair were positioned just above or more commonly, just within the dLGN. In addition to the above arrays, a pair of stimulating electrodes was also placed in the optic chiasm (cf. Chapters 1 and 2) in order to examine the afferent connectivity of corticothalamic and corticocollicular neurons. The responses of cortical cells to electrical stimulation at all of the subcortical sites was photographed from the oscilloscope using a GRASS C4-K camera.

The criteria used to distinguish antidromic from orthodromic activation were based on those of Bishop, Burke and Davis (1962). The main test used was that of impulse collision. Figure 1 shows the general features of antidromic and orthodromic activation of cortical neurons. In the case where the cell's own axon is being stimulated (Part 1 of Fig. 1: antidromic activation), an action potential (closed arrow) resulting from stimulation at S will not be recorded at the cell body (R) if it is generated at the same time, or just after an action potential is initiated in the cell body itself (open arrow). This action potential, travelling orthodromically, will collide with the electrically evoked impulse somewhere between R and S and because of refractoriness in the nerve, neither spike will proceed beyond the collision point. Only if the orthodromic spike has passed the stimulating site

will a spike be initiated at S which can be recorded at R. The experimental way collision is tested is shown in 1A to 1C. The electrical stimulus (black arrow) is triggered by a spontaneous spike or visually evoked spike (open arrow). If the latency of the presumed antidromic action potential is T, then collision will occur when the electrical stimulation is triggered within T'msec after the orthodromic spike is generated (part C). T' represents the antidromic latency (T) plus a fraction of a millisecond related to the refractoriness of the nerve. In B of part 1, the electrically evoked action potential is elicited at a delay greater than T' and the response to electrical stimulation is recorded in the cell body since the orthodromic spike has passed the site of stimulation.

Collision can never occur in the situation shown in Part 2 of Fig. 1, since the spontaneously evoked spike travels along a nerve different from the one being stimulated. Thus when a cell is orthodromically excited, the delay between the orthodromic spike and electrical stimulation can be extremely short (C of part 2) and yet the electrically evoked action potential is still recorded at the cell body.

Other tests were used to confirm that antidromic activation was or was not occurring. These included fractionation of the waveform at high stimulus frequencies (cf. Bishop *et al.*, 1962) and the fixed latency of response of antidromically evoked spikes. Orthodromic action potentials do not normally follow high frequencies and often have considerable variability in their latencies. These two features are primarily due to the interposition of a synapse between the stimulating and recording sites.

As in all experiments, electrolytic lesions were placed at various intervals along the recording penetrations. In many cases, these lesions were made at the point at which a corticocollicular or corticothalamic neuron was isolated (Fig. 7). All electrode tracks were subsequently reconstructed from 40µ Nissl-stained sections. The laminar pattern of areas 17 and 18 was determined using the criteria described in Chapters 1 and 2. The recognition of the 17/18 border zone is discussed further in Chapter 5.

In order to check the anatomical disposition of corticocollicular and corticogeniculate neurons in areas 17 and 18, two adult cats were injected with horseradish peroxidase (HRP), one in the SC and one in the dLGN. Micropipettes were pulled on an electrode puller and the tip broken back to a diameter of approximately 50µm. Injection was achieved under pressure applied through a hypodermic syringe linked to the pipette with fine polythene tubing. A small volume of air separated the injection fluid from a column of water in the tubing and syringe. In both cats, the HRP was the isoenzyme C extracted by Dr. R. Hashke in the laboratories of the Department of Anaesthesiology in the University of Washington, Seattle. Each injection delivered about 1µL of 10% HRP. After 24 hours survival, the animals were anaesthetised with Nembutal and perfused through the heart with lite fix (neutral buffered paraformaldehyde). After perfusion, the blocks of brain were allowed to fix for several hours and then placed to sink in 30% sucrose solution in 0.1 m phosphate buffer. Frozen sections 40µ thick were washed in 0.1 m phosphate buffer, incubated with

diaminobenzadine (D.A.B.) mixture for 15 minutes, mounted on subbed slides and lightly counter stained with cresyl violet.

RESULTS

HORSERADISH PEROXIDASE STUDIES

After a bilateral injection of HRP into the superior colliculus, labelled cells were found in areas 17 and 18 of both hemispheres. Neurons filled with HRP were restricted to lamina V and all appeared to have pyramidal morphology. Examples of labelled cells in lamina V of the parastriate cortex are shown in the dark field micrographs (Fig. 2). In areas of heavy labelling, all of the large and many of the small layer V pyramidal neurons were filled with HRP.

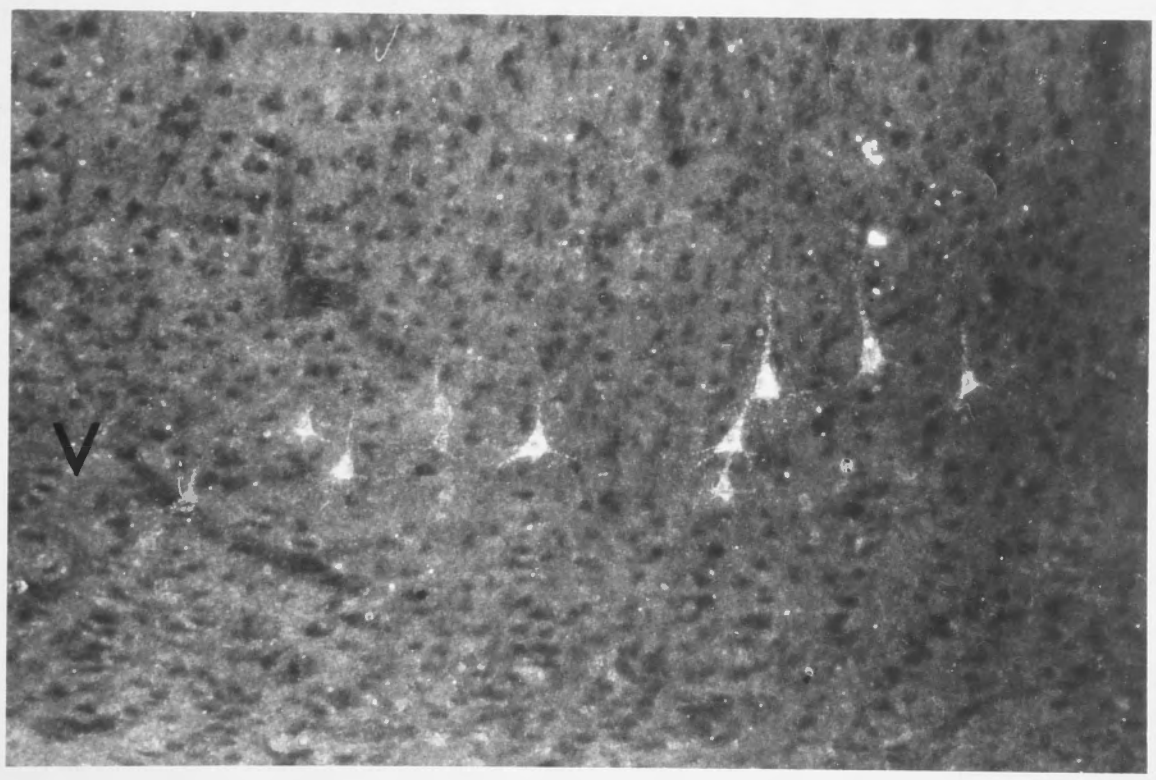
Figure 3 shows the labelling in areas 17 and 18 after an injection of HRP into the dLGN. Small and medium sized pyramids in layer VI of both areas are filled after such an injection. In regions of cortex where the labelling is heaviest, about half of the lamina VI cells contain HRP granules (cf. Gilbert and Kelly, 1975).

The anatomical studies thus confirm previous reports (Gilbert and Kelly, 1975) and show a clear difference in the laminar disposition of corticotectal and corticogeniculate neurons.

NEURONS ANTIDROMICALLY ACTIVATED FROM THE OPTIC RADIATION

A major problem with the technique of electric stimulation is the difficulty in determining exactly what pathways are being stimulated. This is especially true for corticofugal projections to the thalamus and midbrain in that many descending axons pass close to the dLGN before going on to their ultimate

Fig. 2. Dark field photomicrographs of pyramidal cells in lamina V of area 18 labelled with horseradish peroxidase after an injection into the superior colliculus.


V

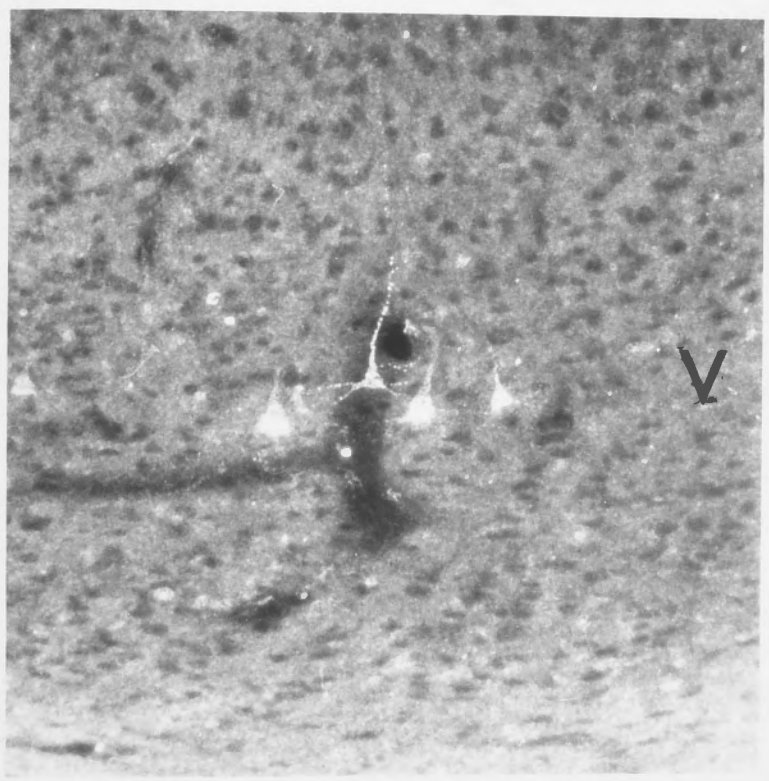
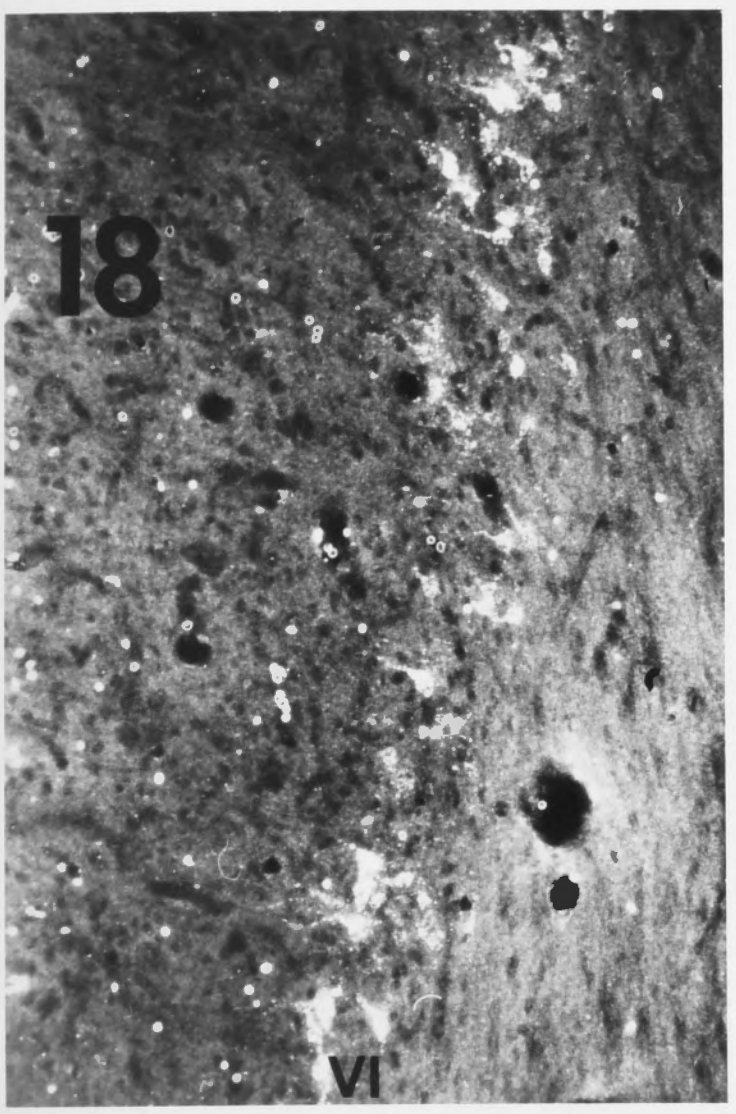
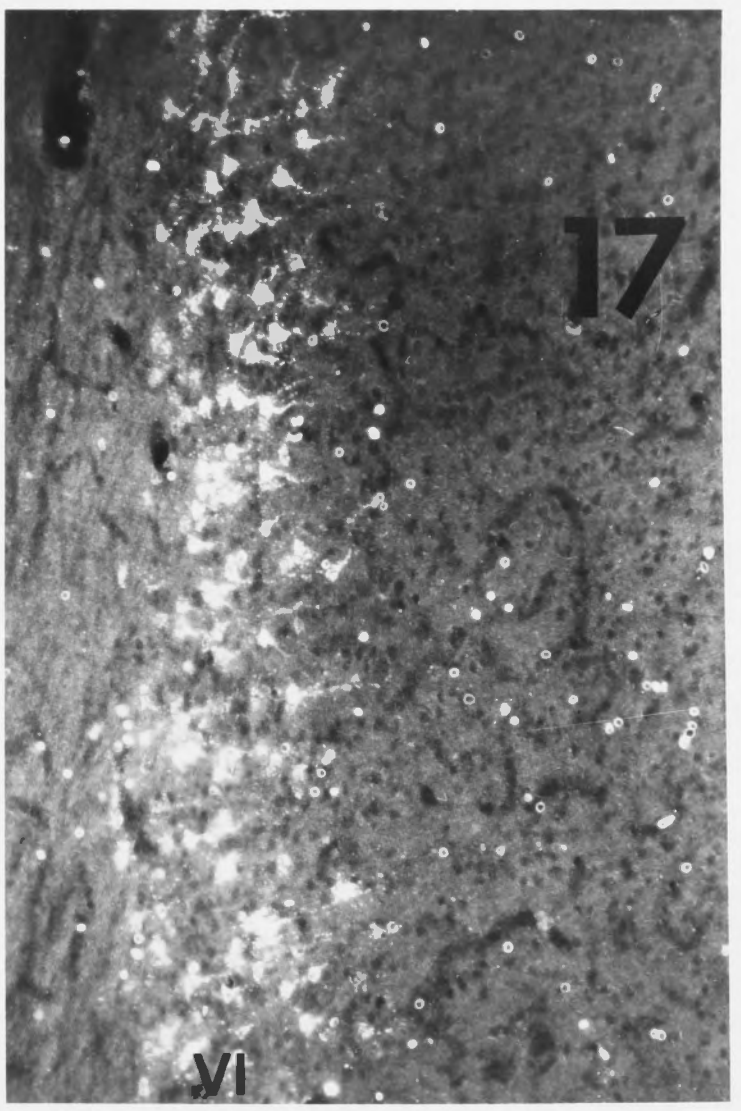

V

Fig. 3. Dark field photomicrographs of pyramidal cells in lamina VI labelled with horseradish peroxidase after an injection into the dorsal lateral geniculate nucleus. A, area 18; B, area 17.


18
VI


17
VI

destination (Garey *et al.*, 1968). Thus antidromic activation produced by electrical stimulation of the dLGN (for example) is, in itself, not sufficient to identify cells efferent to this nucleus. Attempts to define the exact destination of subcortically projecting neurons are discussed at length later in this chapter. In this first section however, discussion is confined to an analysis of the general properties of all cells in area 17 and 18 which were antidromically activated by stimulation of the optic radiation.

Efferent neurons were encountered in 35 cats. In 14 of these animals, only one pair of OR stimulating electrodes was present (placed at AP + 6, lateral 8 and 10 mm, depth 10 to 10.5 mm) and in the other 21 cats, electrodes were also placed in the dLGN and superior colliculus (cf. METHODS).

Receptive field properties

Of the 787 cells isolated in areas 17 and 18, 110 (14%) were antidromically activated from the OR stimulating electrodes. Fifty-seven of these corticofugal neurons were in area 17, 42 in area 18 and 11 were found to be located within the 17/18 border zone (Chapter 5). The receptive fields were plotted for 91 of the 110 efferent cortical neurons. Cells were classed according to their responses to both moving and stationary stimuli (cf. Chapters 1 and 2) and the terminology used in this study is derived from Henry (1977). Thirty-six of the antidromically driven neurons belonged to the S family and 55 had C type receptive fields. One of the S cells and 8 of the C cells possessed the property of end-zone inhibition and were thus classed as S_H and C_H respectively.

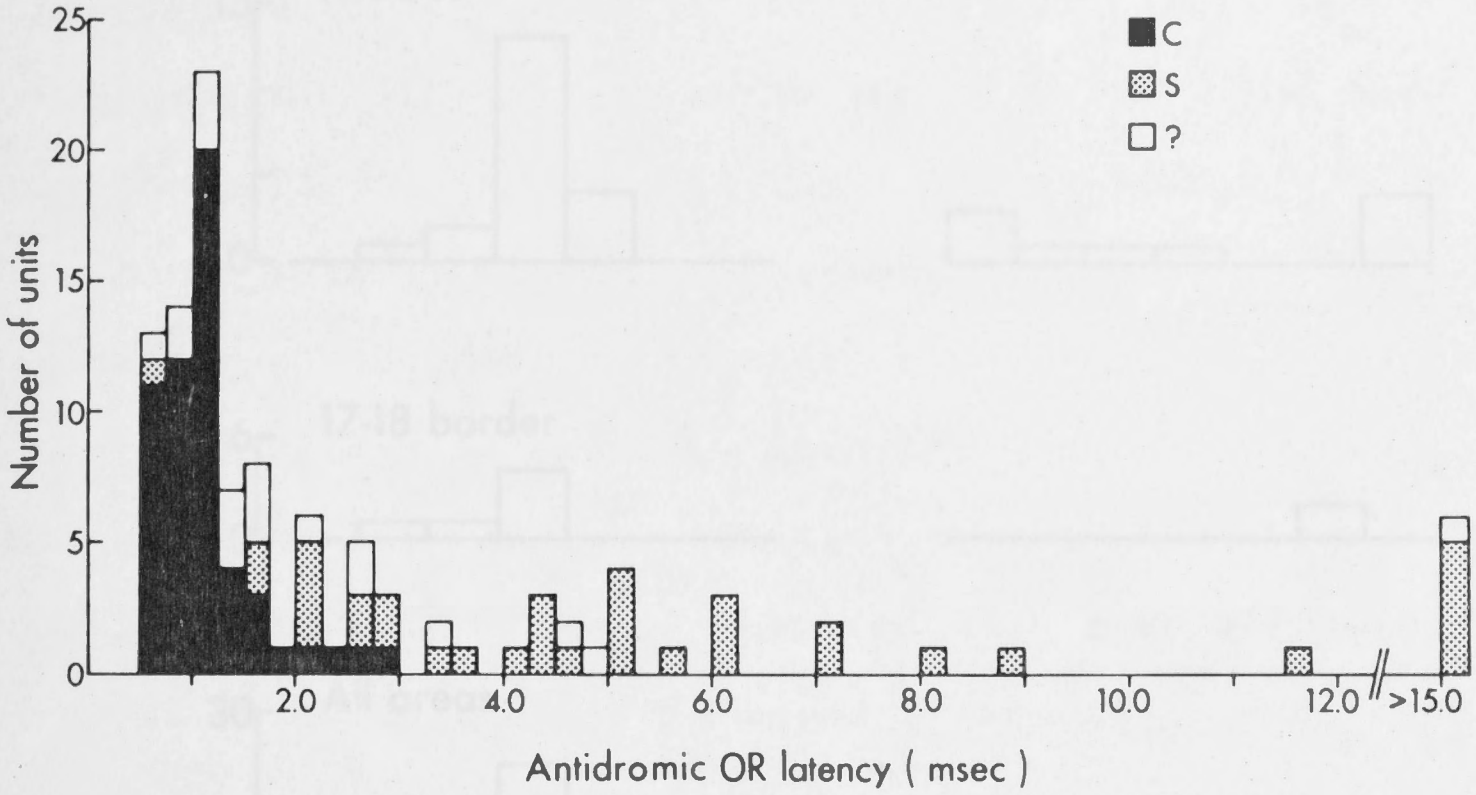


Fig. 4. Antidromic latencies of cells in areas 17 and 18 activated after electrical stimulation of the optic radiation. Filled blocks, cells in the C family (C and C_H); dotted blocks, cells in the S family (S and S_H); open blocks, unclassified cells.

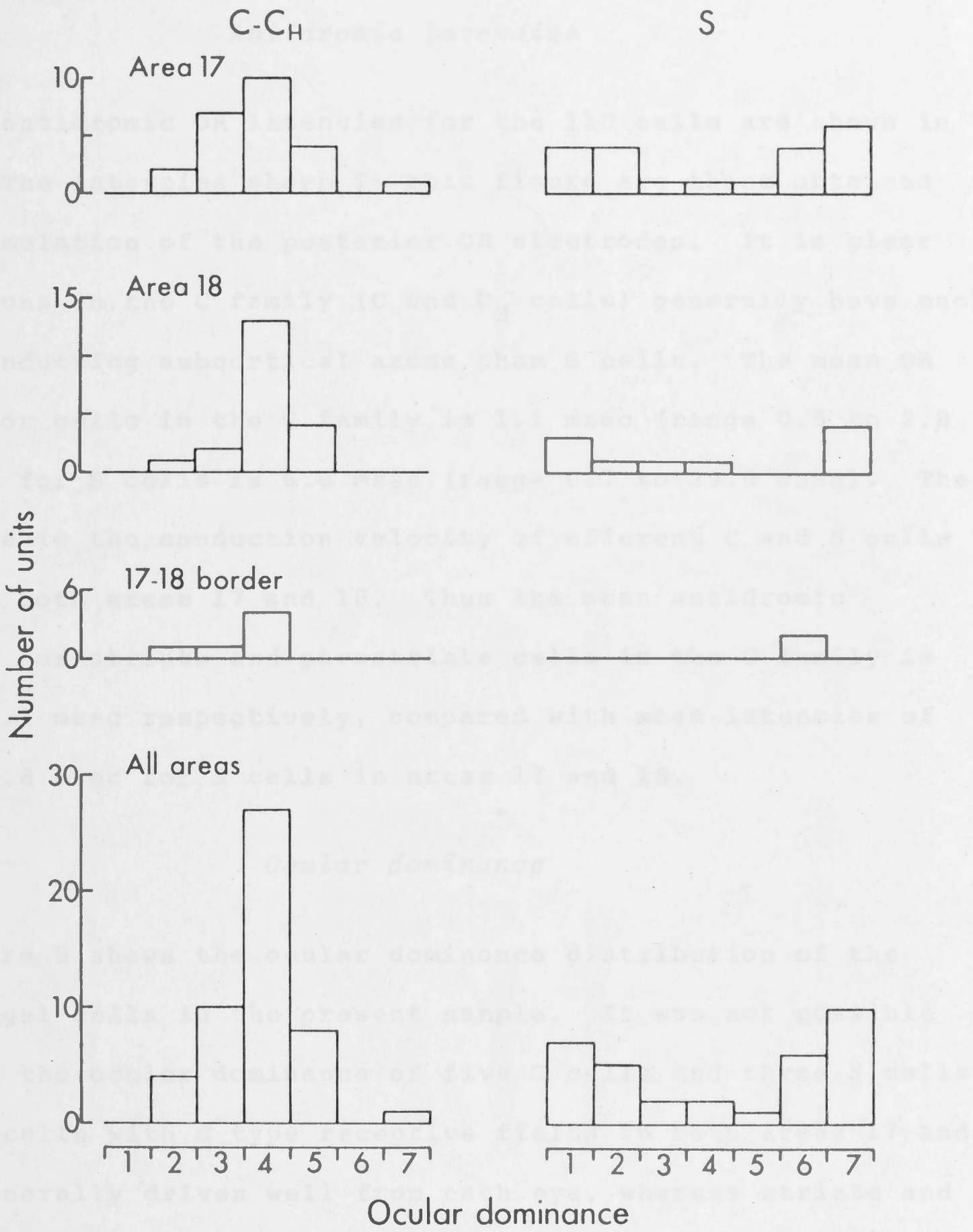


Fig. 5. Ocular dominance distribution of cells antidromically activated from the optic radiation. Dominance groups 1 and 7 represent neurons driven solely by the contralateral and ipsilateral eyes respectively. Cells excited equally from both eyes have an ocular dominance of 4 (cf. Hubel and Wiesel, 1962).

Antidromic latencies

The antidromic OR latencies for the 110 cells are shown in Fig. 4. The latencies shown in this figure are those obtained after stimulation of the posterior OR electrodes. It is clear that neurons in the C family (C and C_H cells) generally have much faster conducting subcortical axons than S cells. The mean OR latency for cells in the C family is 1.1 msec (range 0.5 to 2.8 msec) and for S cells is 6.8 msec (range 0.7 to 29.0 msec). The difference in the conduction velocity of efferent C and S cells holds for both areas 17 and 18. Thus the mean antidromic latencies for striate and parastriate cells in the C family is 1.0 and 1.1 msec respectively, compared with mean latencies of 6.3 and 7.8 msec for S cells in areas 17 and 18.

Ocular dominance

Figure 5 shows the ocular dominance distribution of the corticofugal cells in the present sample. It was not possible to assess the ocular dominance of five C cells and three S cells. Efferent cells with C type receptive fields in both areas 17 and 18 are generally driven well from each eye, whereas striate and parastriate S cells are commonly monocular or only weakly binocular. Considering the overall ocular dominance distribution of cells in the C and S families, 52% of S cells were monocularly discharged compared with only 2% for C and C_H cells.

Laminar Distribution

The laminar distribution of corticofugal S, S_H, C and C_H cells is presented in Fig. 6. The lamina IVa-IVb subdivision

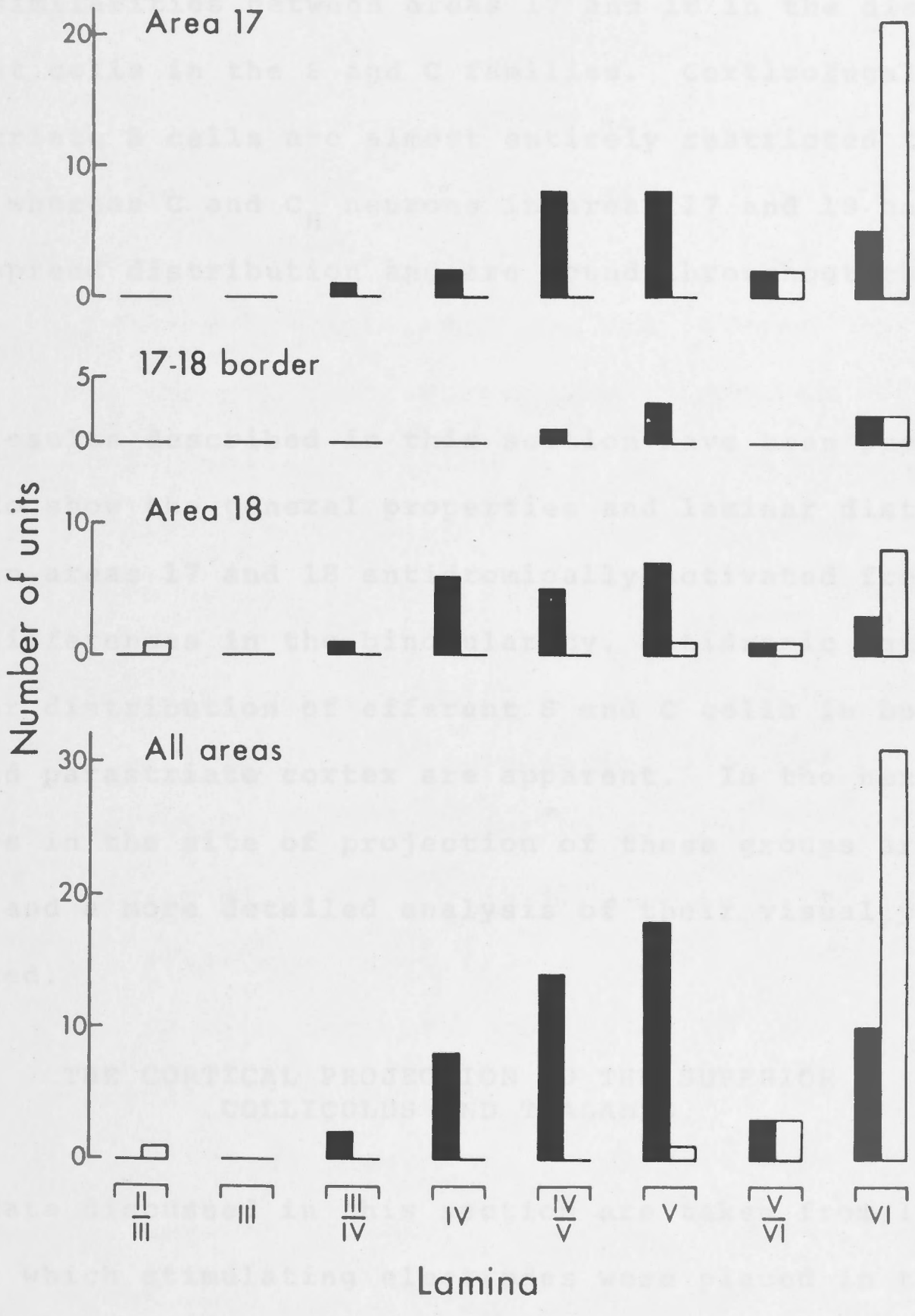


Fig. 6. Laminar distribution of cells antidromically activated from the optic radiation. Filled blocks, C and C_H cells; open blocks, S and S_H cells.

of the parastriate cortex (Chapter 2) is not shown here. Again note the similarities between areas 17 and 18 in the disposition of efferent cells in the S and C families. Corticofugal striate and parastriate S cells are almost entirely restricted to lamina VI whereas C and C_H neurons in areas 17 and 18 have a more widespread distribution and are found throughout the deeper layers.

The results described in this section have been presented in order to show the general properties and laminar distribution of cells in areas 17 and 18 antidromically activated from the OR. Distinct differences in the binocularity, antidromic latencies and laminar distribution of efferent S and C cells in both the striate and parastriate cortex are apparent. In the next section, differences in the site of projection of these groups are described and a more detailed analysis of their visual properties is presented.

THE CORTICAL PROJECTION TO THE SUPERIOR COLLICULUS AND THALAMUS

The data discussed in this section are taken from 19 of the 21 cats in which stimulating electrodes were placed in the OR, SC and in or close to the dLGN. In these 19 animals, efferent cells could be antidromically activated at reasonably low thresholds from both SC and dLGN. Two cats in which there was no collicular activation have not been included in this analysis.

Seventy-nine cells were antidromically activated from the subcortical stimulating electrodes. Thirty-four of these units were driven from the SC of which 32 were also activated from the OR. The observation that many corticocollicular units are

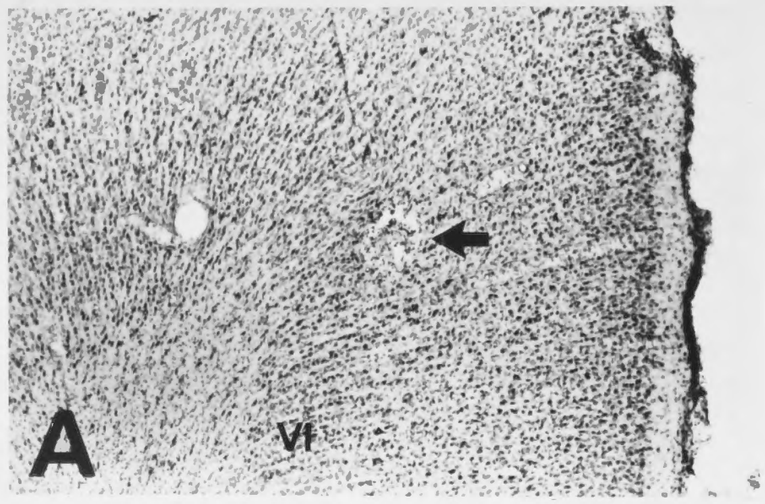
driven from the OR is consistent with the anatomical observation that these fibres pass close to the dLGN on their way to the tectum (Garey *et al.*, 1968). The remaining 45 corticofugal cells were activated after stimulation of the OR but could not be excited from the colliculus. Twenty-four of these neurons were excited from both OR stimulating sites, 7 were driven only from the anterior pair and 14 were activated exclusively from the posterior electrodes. In other words, 31 of the corticofugal cells not stimulated from the SC were antidromically driven from the stimulating electrodes placed just above or more typically just within the dLGN.

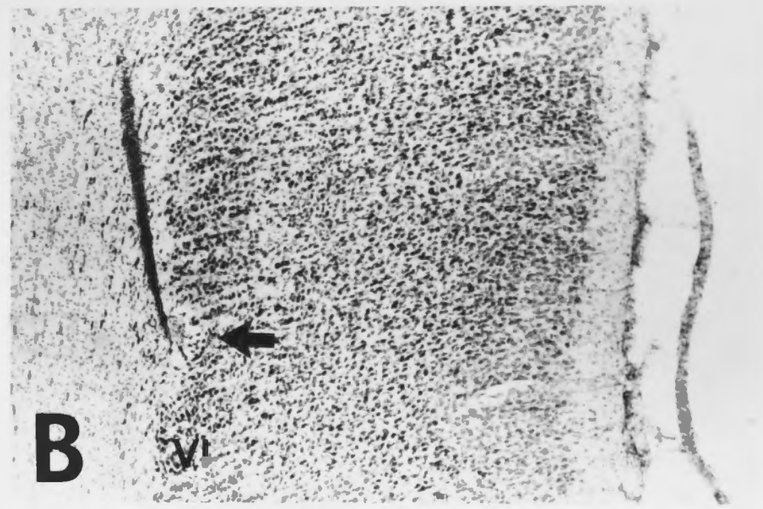
As mentioned earlier, the majority of corticotectal fibres are also activated from the optic radiation and care must be taken to distinguish between stimulation of axon terminals and activation of fibres of passage. It is possible for example, that some of the cells activated from the anterior OR electrodes but not from the SC are, in fact, projecting to the pons (Garey *et al.*, 1968; Brodal, 1972, a,b; Sanides *et al.*, 1978), rather than the thalamus. Since layer V projects to the pontine nuclei and the thalamic regions medial to the dLGN, whereas layer VI sends axons to the dLGN (see INTRODUCTION), important indications as to the site of projection of antidromically activated cells can be obtained by studying the distribution of these cells within the various cortical laminae.

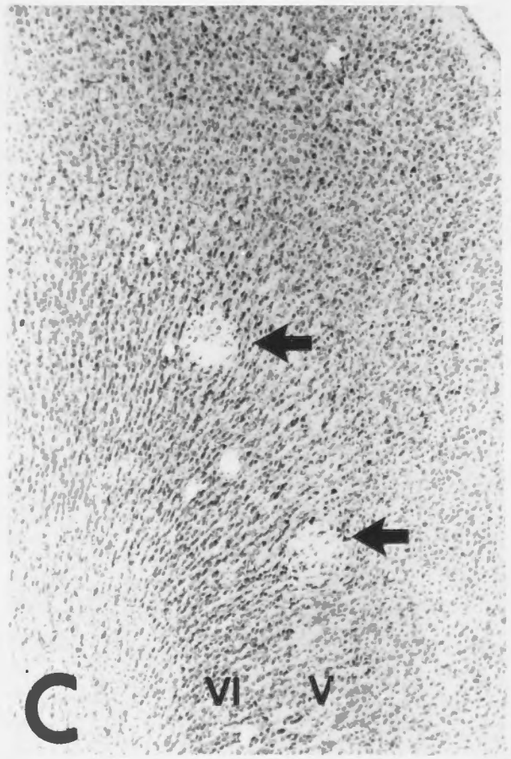
Laminar distribution of cells activated from SC or OR

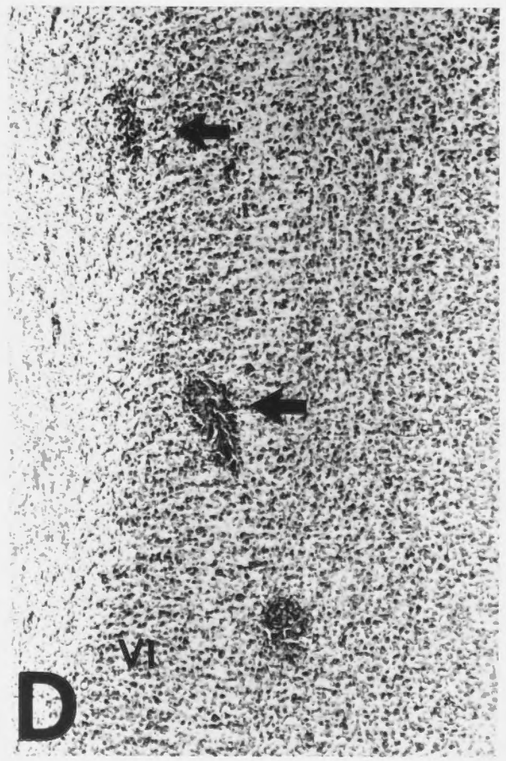
Many antidromically activated cells were marked with electrolytic lesions. Some examples of these are presented in

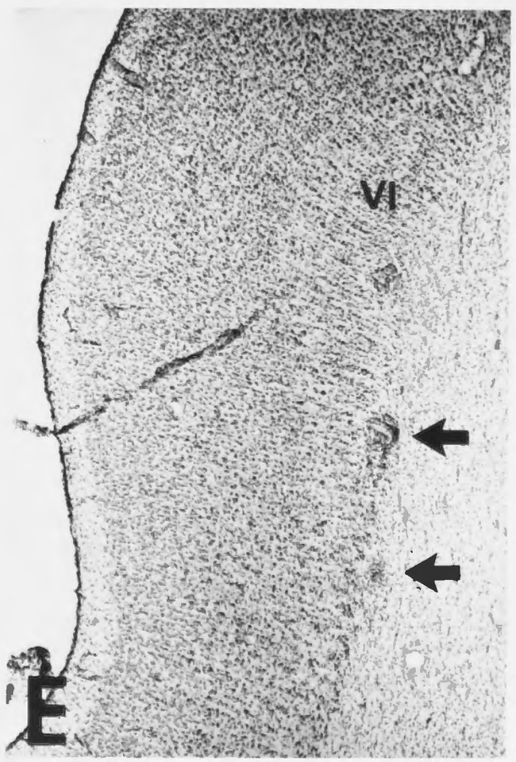
Fig. 7. Photomicrographs of electrode penetrations in the lateral gyrus of the cat. Arrows show the location of efferent cells marked with electrolytic lesions. All arrows denote the position of corticothalamic neurons with the exception of the bottom lesion in C which shows the location of a corticocollicular cell. A-D, penetrations in the medial bank (area 17); E, penetration in the lateral bank (mostly area 18).


A
VI


B
VI


C
VI
V


D
VI


VI
E

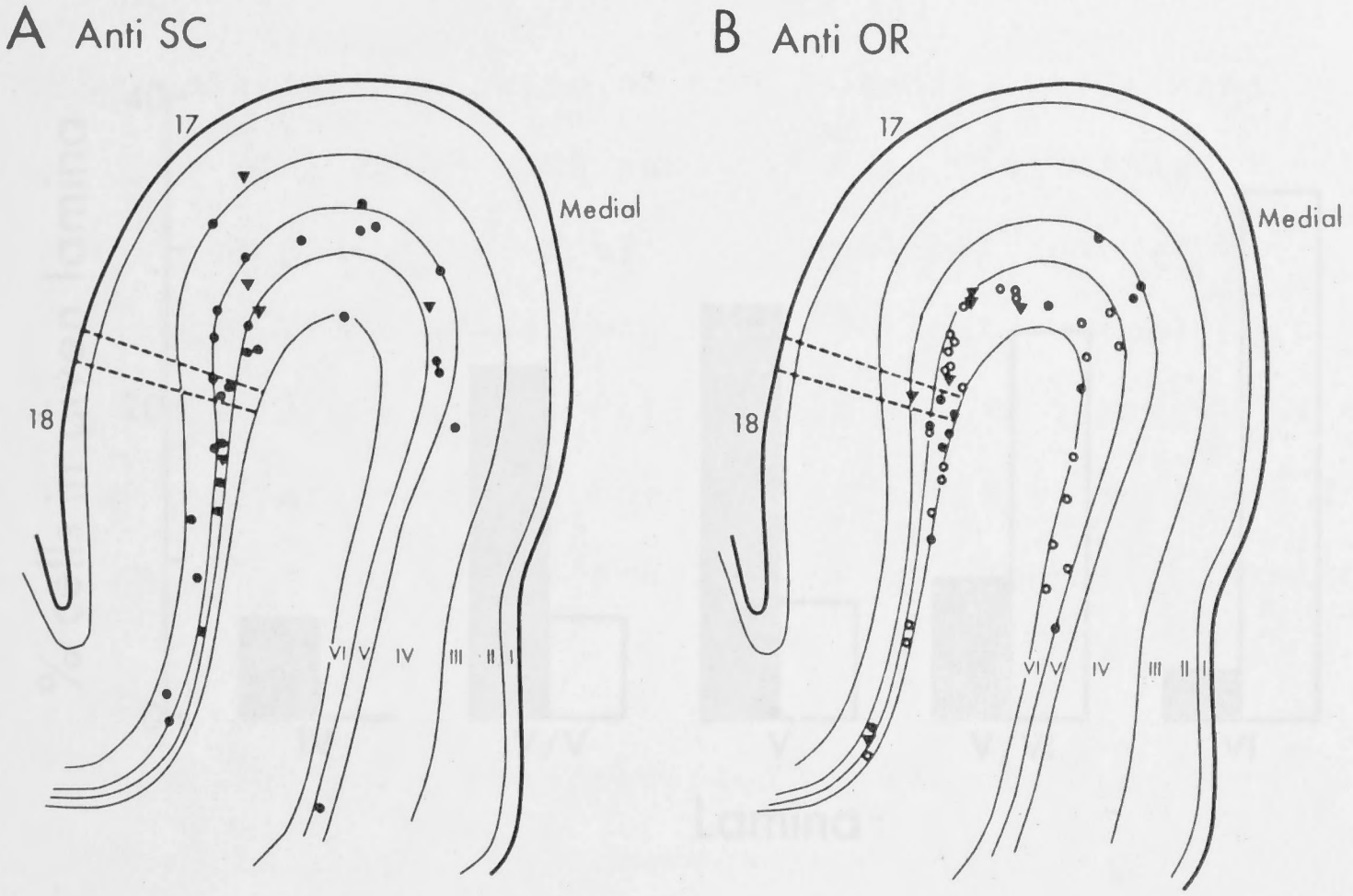


Fig. 8. Schematic representation of the left lateral gyrus showing the laminar disposition of corticofugal cells. A, cells antidromically activated from the superior colliculus; B, cells antidromically activated from the optic radiation. Area within dotted lines represents 17/18 border zone. Filled circles, C and C_H cells; open circles, S cells; closed triangles, unclassified cells.

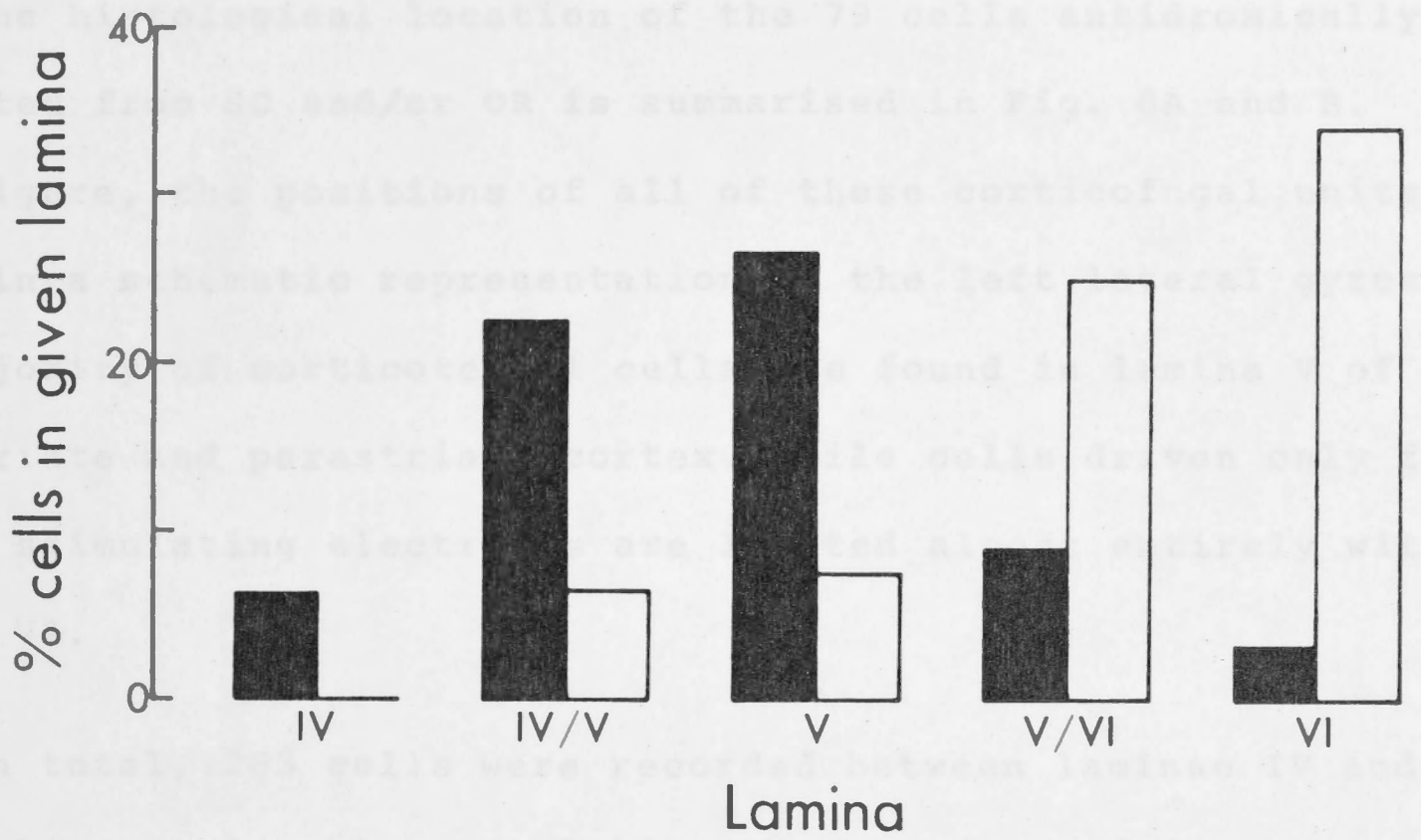


Fig. 9. The proportions of cells with efferent axons in each cortical lamina. Data pooled from areas 17 and 18. Filled blocks, cells antidromically activated from the superior colliculus; open blocks, cells antidromically activated from the optic radiation.

Fig. 7; micrographs A to D show electrode penetrations in the medial bank of the lateral gyrus (area 17) and Fig. 7E shows a track in the lateral bank of the lateral gyrus (area 18).

The histological location of the 79 cells antidromically activated from SC and/or OR is summarised in Fig. 8A and B. In this figure, the positions of all of these corticofugal units are shown in a schematic representation of the left lateral gyrus. The majority of corticotectal cells are found in lamina V of both the striate and parastriate cortex, while cells driven only from the OR stimulating electrodes are located almost entirely within lamina VI.

In total, 283 cells were recorded between laminae IV and VI in the 19 cats in which SC electrodes were in position. For each lamina, the proportion of neurons antidromically activated from SC or OR was then calculated and expressed as a percentage of the total number of cells encountered in that layer. The results are shown in Fig. 9; data from both area 17 and area 18 have been pooled. It is clear that corticotectal neurons are encountered most often at the IV/V border and in layer V, whereas cells antidromically activated exclusively from the OR stimulating electrodes are commonly found at the V/VI border and in lamina VI. These reults should be compared with HRP studies (Gilbert and Kelly, 1975; Figs. 2 and 3, this chapter) which indicate that layer V pyramidal cells project to the SC while layer VI neurons are efferent to the dLGN. Since the majority of cells antidromically driven from the electrodes within the dLGN were in layer VI, it is reasonable to conclude that their axons are

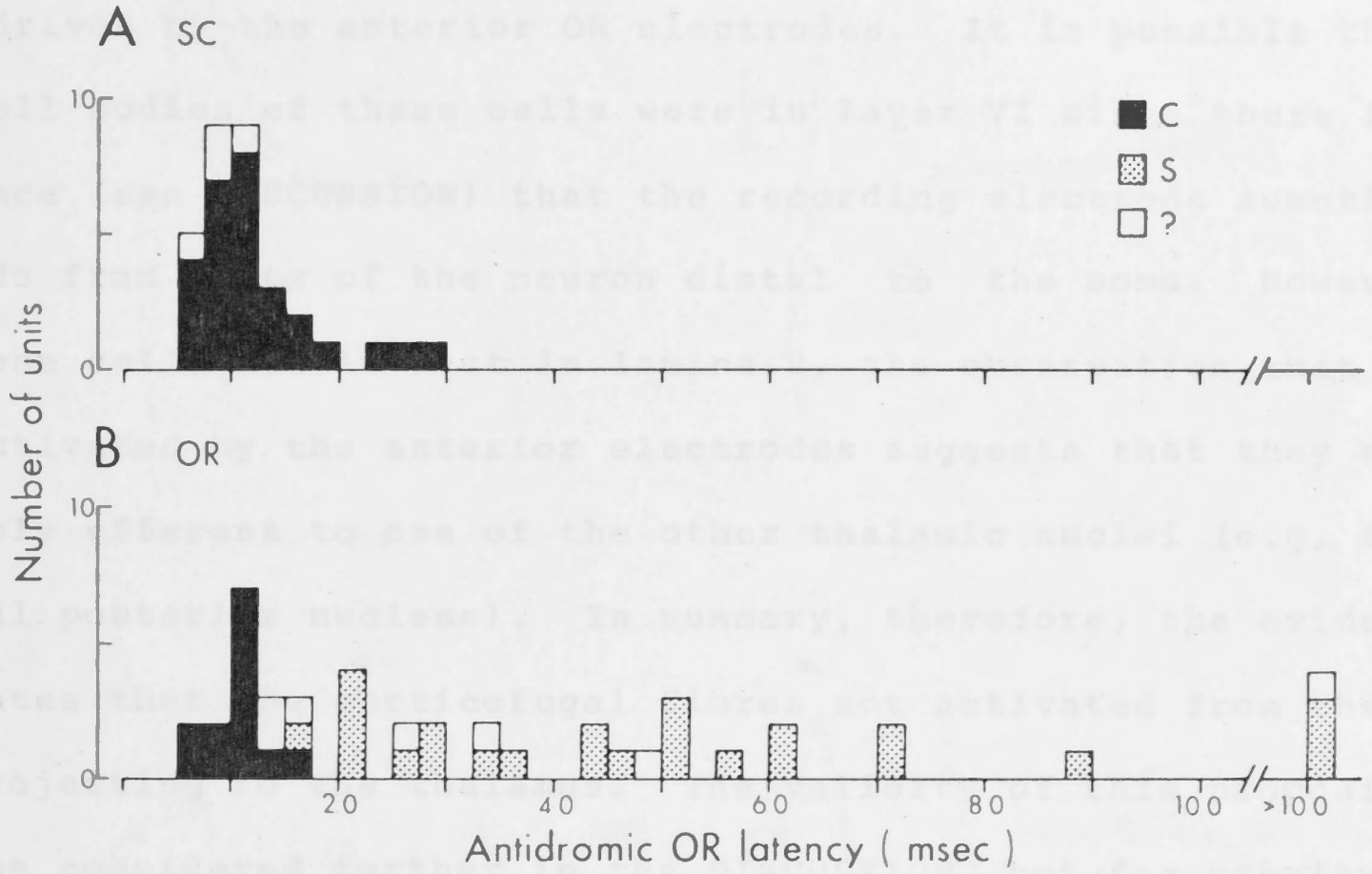


Fig. 10. Antidromic latencies of corticocollicular and cortico-thalamic neurons obtained after electrical stimulation of the optic radiation. A, cells also activated from the superior colliculus; B, cells activated only from the optic radiation. Filled blocks, cells in the C family; dotted blocks, S cells; open blocks, unclassified cells.

mostly corticogeniculate and are not passing on to other subcortical areas.

Of the 4 cells in lamina V activated from OR but not SC, 3 were driven by the anterior OR electrodes. It is possible that the cell bodies of these cells were in layer VI since there is evidence (see DISCUSSION) that the recording electrode sometimes records from parts of the neuron distal to the soma. However if these cells are in fact in lamina V, the observation that they are activated by the anterior electrodes suggests that they are probably efferent to one of the other thalamic nuclei (e.g. the lateral posterior nucleus). In summary, therefore, the evidence indicates that the corticofugal fibres not activated from the SC are projecting to the thalamus. The validity of this proposition will be considered further in the DISCUSSION, but for brevity, cells activated from OR but not SC will be described as corticothalamic in the remainder of this analysis.

Antidromic latencies of corticocollicular and corticothalamic cells

The antidromic OR latencies for the corticocollicular and presumed corticothalamic neurons in the striate and parastriate cortex are shown in Fig. 10. Most of the latencies shown are those obtained after stimulation of the posterior OR electrode pair. It is clear that cells in the C family whether they are projecting to the tectum or to the thalamus, generally have faster conducting axons than corticothalamic S cells (cf. Fig. 4). The relatively small number of more slowly conducting C cells are all efferent to the SC.

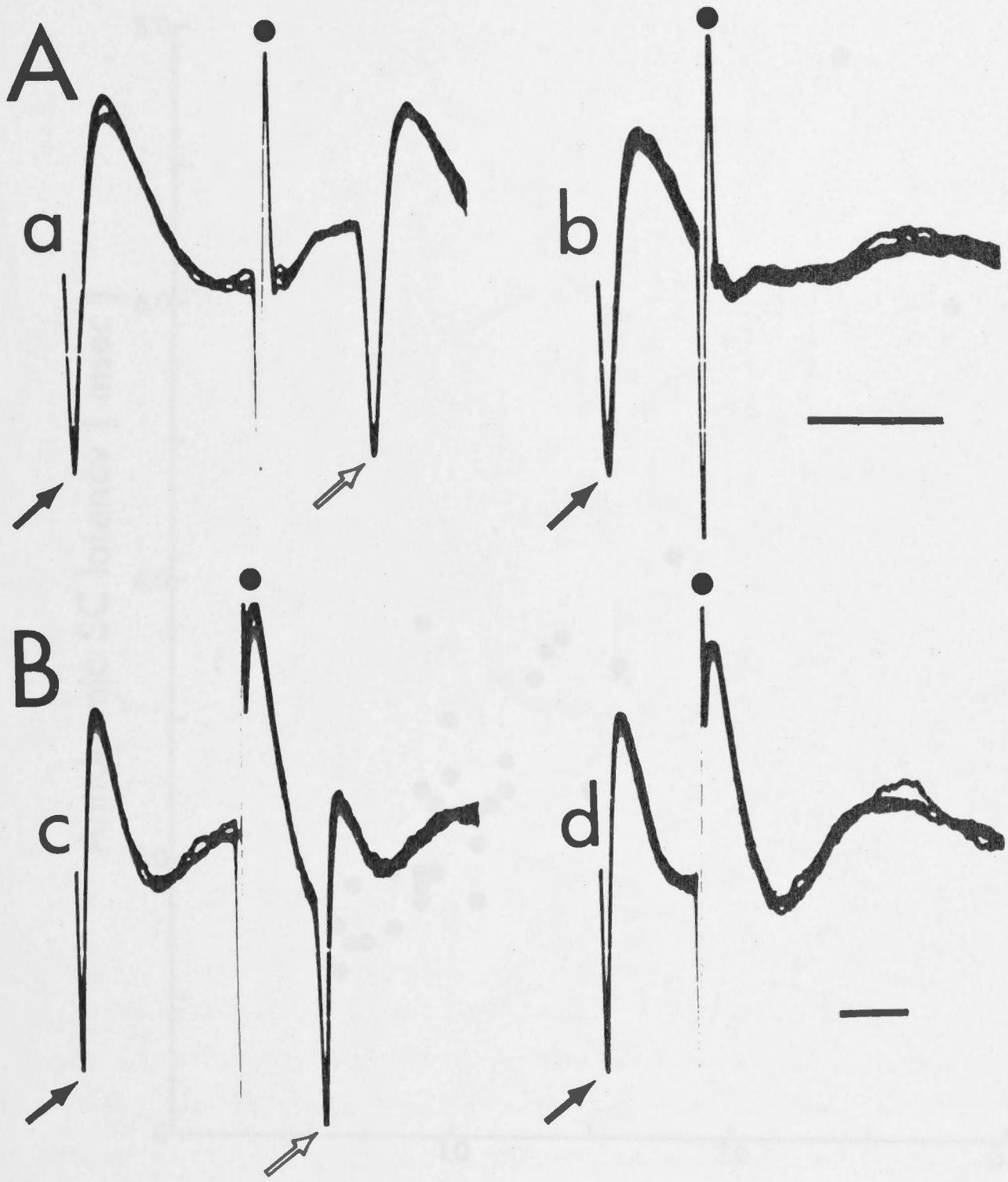


Fig. 11. Antidromic activation of C cell in lamina V of area 17. A: electrical stimulation of OR, collision of antidromic spike. B: electrical stimulation of SC, collision of antidromic spike. Filled arrow, orthodromic spike; open arrow, antidromic spike; filled circle, stimulus artifact. Time marker: A, 2 msec; B, 2 msec.

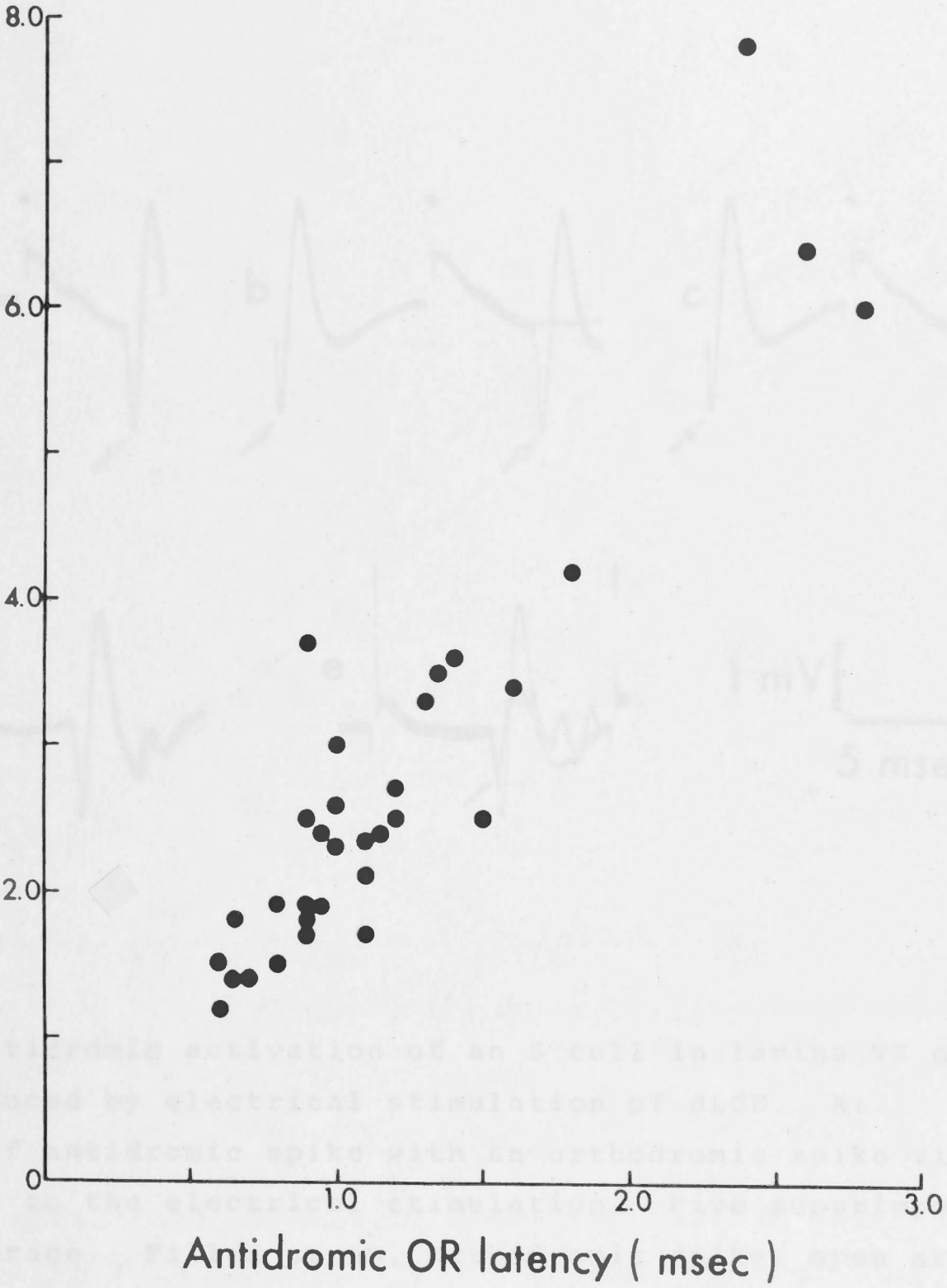


Fig. 12. Antidromic latencies of corticocollicular neurons activated from both the optic radiation (OR) and superior colliculus (SC).

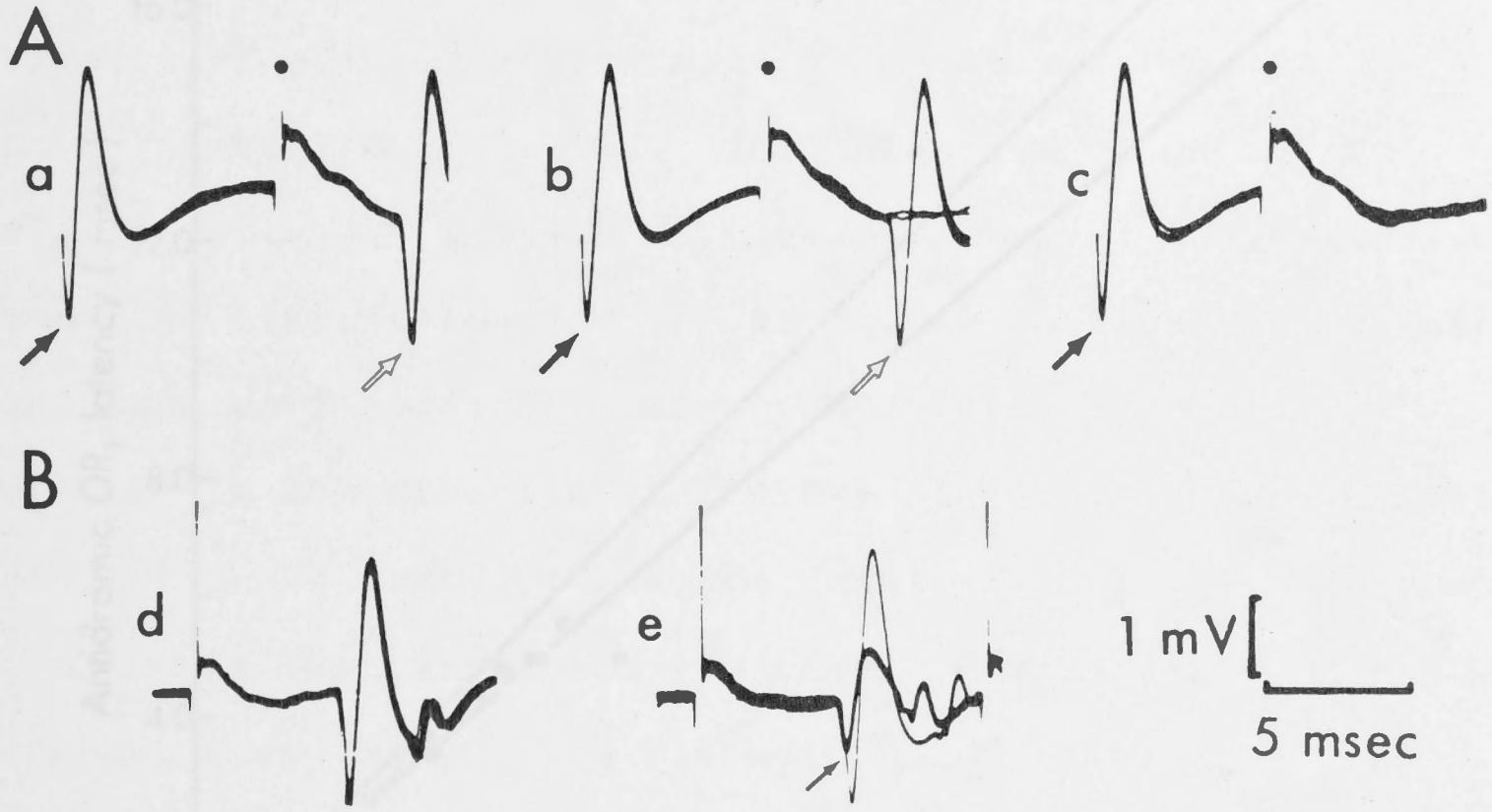


Fig. 13. Antidromic activation of an S cell in lamina VI of area 17 produced by electrical stimulation of dLGN. A: collision of antidromic spike with an orthodromic spike visually evoked prior to the electrical stimulation. Five superimposed trials per trace. Filled arrow, orthodromic spike; open arrow, antidromic spike; filled circle, stimulus artifact. B: d, fixed latency of response; e, fractionation (small arrow) of antidromic waveform at high rates of stimulation; d, 10 Hz; e, 100 Hz.

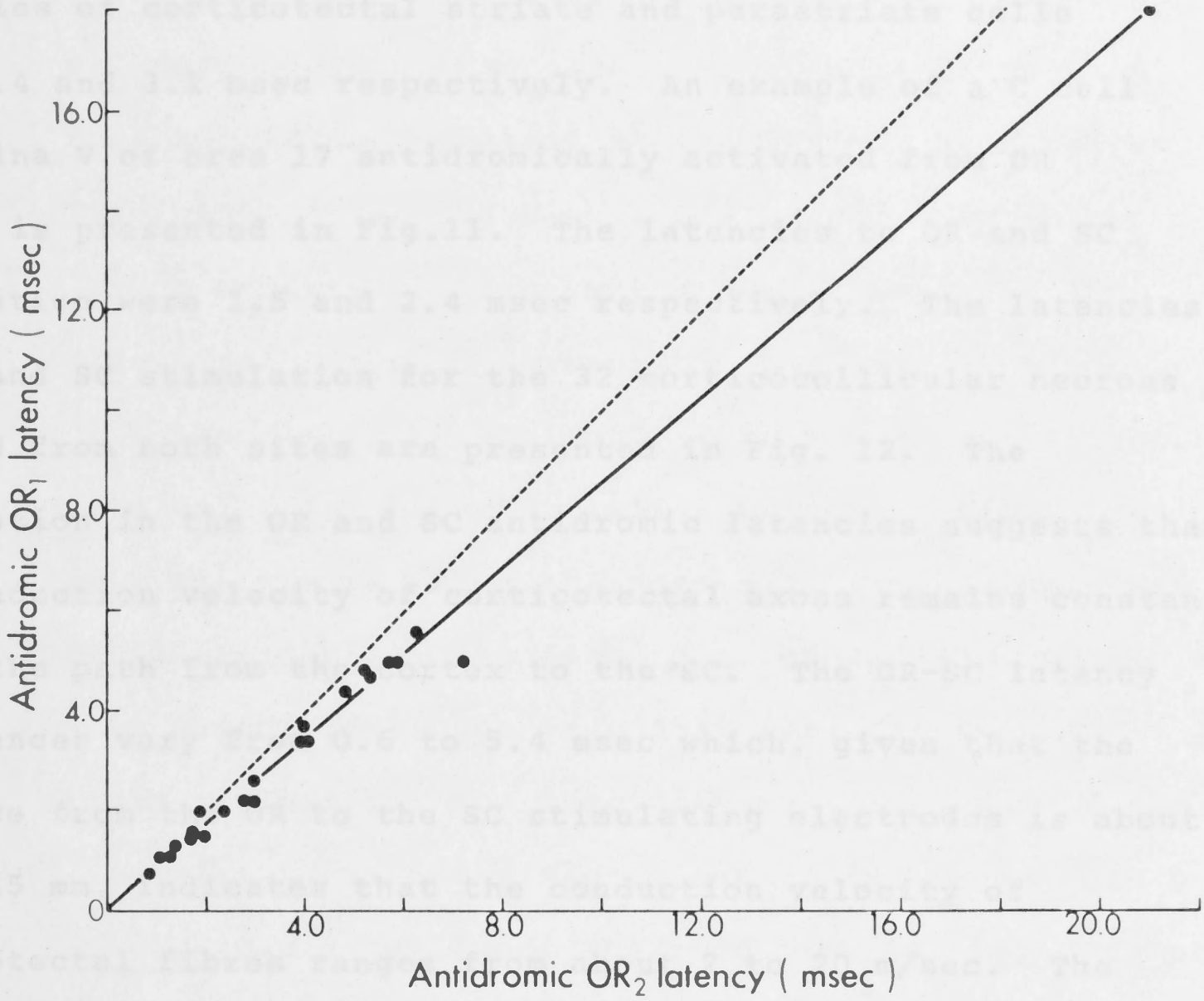


Fig. 14. Antidromic latencies of corticothalamic neurons activated from both pairs of optic radiation stimulating electrodes. OR_1, posterior pair; OR_2, anterior pair positioned just above, or more usually just within the dLGN. Dashed line, expected latencies if both pairs are in the same position; solid line, regression line through experimental points.

The mean SC latency for the 34 corticocollicular neurons was 2.6 msec with a range of 1.2 to 7.8 msec. The mean SC latencies of corticotectal striate and parastriate cells were 2.4 and 3.1 msec respectively. An example of a C cell in lamina V of area 17 antidromically activated from OR and SC is presented in Fig.11. The latencies to OR and SC stimulation were 1.5 and 2.4 msec respectively. The latencies to OR and SC stimulation for the 32 corticocollicular neurons excited from both sites are presented in Fig. 12. The correlation in the OR and SC antidromic latencies suggests that the conduction velocity of corticotectal axons remains constant along the path from the cortex to the SC. The OR-SC latency differences vary from 0.6 to 5.4 msec which, given that the distance from the OR to the SC stimulating electrodes is about 12 to 15 mm, indicates that the conduction velocity of corticotectal fibres ranges from about 2 to 20 m/sec. The majority of axons from corticocollicular neurons are fast conducting and therefore of large diameter and most of the information being transmitted from the cortex reaches the colliculus in less than 3 msec.

Figure 13 shows antidromic activation of a lamina VI S cell in area 17 produced by electrical stimulation of the dLGN. The long latency (5.0 msec) is characteristic of corticofugal S cells. As described earlier, two pairs of stimulating electrodes were placed in the optic radiations, one in the OR itself and one just above or more usually just in the dLGN. Figure 14 shows the antidromic latencies for corticothalamic neurons stimulated from both sites. OR_1 refers to the posterior and OR_2 to the anterior pairs. The dashed line represents what

would be expected if the two pairs were in the same position and the solid line is the regression line through the experimental points. It can be seen that the longer absolute antidromic latencies are correlated with greater differences between OR_1 and OR_2. This result is important in that it has been suggested (e.g. Guillery, 1967) that the fine axons in the dLGN which degenerate after cortical lesions may be collaterals of the coarser corticofugal fibres. However the increase in the OR_1-OR_2 difference for long latency corticothalamic axons (all of which originate from cells in layer VI) indicates that these fibres conduct slowly all the way from the cortex to the thalamus and are entirely independent of the fast corticofugal system. This observation is supported by the fact that fast and slow corticothalamic neurons tend to have different receptive field properties, S cells having more slowly conducting axons than C cells (Fig. 10). One S cell, not shown in Fig. 14, had OR_1 and OR_2 latencies of 23.0 and 29.0 msec respectively. This latency difference, when considered along with the absolute OR_1 antidromic latency, suggests that the conduction velocity of this S cell's axon was only about 0.5 m/sec.

Receptive field properties of corticocollicular and corticothalamic neurons

Corticocollicular neurons

Of the 34 corticotectal neurons identified in the striate and parastriate cortex, 29 could be classed according to their responses to visual stimuli. *All* of the classified units, in both areas 17 and 18, belonged to the C family. Nineteen of these cells were in area 17, 9 in area 18 and 3 were located

within the 17/18 border zone. Most of the classified corticotectal neurons had receptive fields within 5^{o} of the area centralis.

Palmer and Rosenquist (1974) have reported that corticotectal units lack any clear summation along the line of optimal orientation and respond very well to small moving spots. In the present study, qualitative testing revealed that although many corticocollicular cells were similar to those described by Palmer and Rosenquist, a significant number did not respond to small stimuli but were optimally excited by long (5^{o} or more) edges or bars. These cells thus showed summation with increasing stimulus length. In addition, 4 of the efferent C cells had clear end-zone inhibitory regions and were thus classed as C_{H}. The relative proportions of the various types of corticocollicular C cells are shown in Table 1.

In total, 22 corticotectal C cells were tested with stimuli or various lengths; 10 resembled the Palmer and Rosenquist (1974) cell, 4 were C_{H} and 8 preferred elongated stimuli. All corticotectal cells were broadly tuned for stimulus orientation and had a relatively high spontaneous discharge. The majority responded to both slow and fast stimulus movements, although efferent C cells in area 18 generally responded more reliably to very fast movements.

Six corticotectal neurons responded equally well to optimally oriented stimuli moved in either direction. The remainder (23: 79%) showed various degrees of directional specificity. Seventeen of these units were completely or almost completely direction selective in that movement in the non-

TABLE 1

Corticocollicular neurons

	AREA		
	17	17/18	18
C: Palmer and Rosenquist type	7	0	3
C: Responsive to long edges	4	2	2
C: End stopped (C_H)	2	0	2
C: Not tested	4	1	2
Not classified	4	0	1

preferred direction evoked no or only minimal response. Of the 10 C cells which showed little or no length summation, 9 were highly selective for the direction of stimulus movement. In contrast, of the 8 C cells which responded optimally to long edges, 4 showed no direction specificity and 2 were only weakly selective. These results suggest that there is a correlation between the degree of length summation and the amount of direction selectivity in corticotectal neurons. Furthermore, the mean antidromic SC latency for Palmer and Rosenquist type C cells was shorter (2.8 msec) than for C cells which responded best to elongated stimuli (mean 3.6 msec).

The ocular dominance of corticocollicular cells is shown in Fig. 15B. It was not possible to accurately assess the ocular dominance of 5 corticotectal neurons, but all had binocular receptive fields. In total therefore, 28 of the 29 visually characterised corticocollicular units in areas 17 and 18 were binocularly discharged by visual stimulation. The majority of these binocular cells were driven about equally by the two eyes (Fig. 15B). This result is very much in agreement with that of Palmer and Rosenquist (1974).

In general the receptive fields of striate and parastriate corticocollicular C cells are very similar. The major difference is the size of the receptive fields; the mean area of the receptive fields of area 17 corticotectal neurons was 6.6 square degrees compared with 11.7 square degrees for parastriate cells. Since most of the receptive fields in the present sample were located within 5^{o} of the area centralis, this difference is not related to the eccentricity of striate and parastriate neurons.

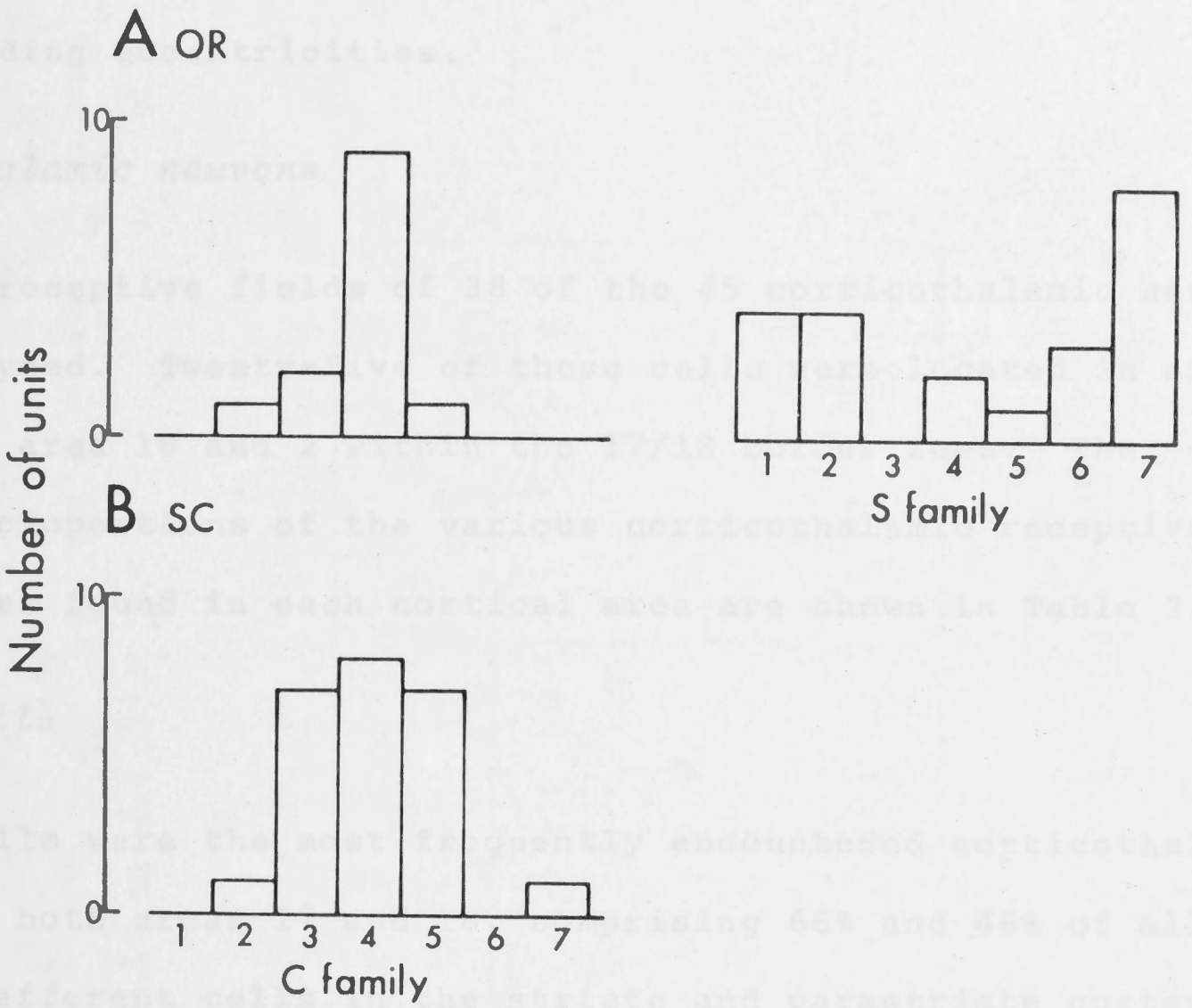


Fig. 15. Ocular dominance distribution of corticotectal and corticothalamic cells. A, cells antidromically activated only from the optic radiation; B, cells antidromically activated from the superior colliculus.

The receptive fields of corticotectal cells in both visual areas are generally larger than the fields of other cells at corresponding eccentricities.

Corticothalamic neurons

The receptive fields of 38 of the 45 corticothalamic neurons were analysed. Twenty-five of these cells were located in area 17, 11 in area 18 and 2 within the 17/18 border zone. The relative proportions of the various corticothalamic receptive field types found in each cortical area are shown in Table 2.

(1) *S cells*

S cells were the most frequently encountered corticothalamic neuron in both areas 17 and 18, comprising 66% and 46% of all thalamic efferent cells in the striate and parastriate cortex respectively. Efferent S cells in both areas generally had no or only low spontaneous activity, were sharply tuned for stimulus orientation and responded best to slow stimulus movements (although parastriate S cells usually preferred slightly faster velocities). With regard to these properties, corticothalamic S cells are therefore similar to other non-efferent S cells (cf. Chapter 1, Chapter 2). Further, the receptive fields of subcortically projecting S cells appeared to be about the same size as the rest of the S population.

One important difference in the visual properties of efferent and non-efferent S cells is the degree of direction selectivity in the two groups. In the striate cortex, 18 of the 19 cortico-thalamic S cells were completely or almost completely selective for the direction of movement of an optimally oriented stimulus.

TABLE 2

Corticothalamic neurons

		AREA		
		17	17/18	18
S		19	0	6
C	Palmer and Rosenquist type	3	1	1
C	Responsive to long edges	1	1	1
C	Not tested	2	0	3
	Not classified	4	1	2

In total, 42 S cells in laminae V/VI and VI showed marked directional specificity, hence 43% of these units (18/42) were antidromically activated from the optic radiation. In contrast, only one of the 8 (12%) layer VI S cells which exhibited no or only weak directional specificity had a corticothalamic axon.

The pattern is very similar in area 18. All 6 corticothalamic neurons from this area were highly selective for the direction of movement of an optimally oriented stimulus. Of the 12 S cells in laminae V/VI and VI which were completely or almost completely direction selective 6 (50%) were antidromically activated, whereas none of the four weakly direction selective neurons in these layers had efferent axons.

The ocular dominance distribution of corticothalamic striate and parastriate S cells is shown in Fig. 15A. Out of the 22 cells for which ocular dominance could be satisfactorily determined, 12 (55%) had monocular receptive fields. This distribution is almost identical in areas 17 and 18; 54% of striate corticothalamic S cells were monocular compared with 60% of parastriate neurons. There is a slight tendency for cells driven by the ipsilateral eye (ocular dominance group 7) to have corticothalamic axons more often than other dominance groups. In area 17 at least, this may be related to the fact that S cells with receptive fields in the ipsilateral eye are most common in layer VI (Chapter 1). However, within lamina VI itself, there is no clear indication that striate S cells in ocular dominance groups 6 and 7 give rise to corticothalamic axons more often than cells driven by the contralateral eye. In area 17, 43% of all layer VI S cells in ocular dominance groups 1 and 2 were

antidromically activated compared with 44% of S cells in groups 6 and 7.

(2) *C cells*

Thirteen C cells were antidromically activated from the stimulating electrodes in the optic radiation but were not driven from the SC (Table 2). Five of these cells resembled the Palmer and Rosenquist cell and three others fired optimally to elongated stimuli. Like corticocollicular cells, the presumed corticothalamic C cells commonly had high spontaneous activity, were broadly tuned for orientation and continued to respond at high stimulus velocities. Nine of the 13 C cells were completely or almost completely direction selective.

The ocular dominance distribution of these C cells is shown in Fig. 15A. All were binocular and their distribution is very similar to that of corticocollicular C cells (Fig. 15B). The binocularity of corticothalamic C cells is in marked contrast to the high degree of monocularity exhibited by efferent S cells.

The relative proportions of efferent S and C cells

Evidence presented earlier indicates that about 30% of the cells in lamina V project to the tectum and that 34% of lamina VI neurons are efferent to the thalamus (Fig. 9). These proportions were determined by comparing the number of corticofugal cells with the *total* number of units isolated in a given lamina. It is of interest to know how many cells *in a given receptive field class* give rise to corticofugal axons.

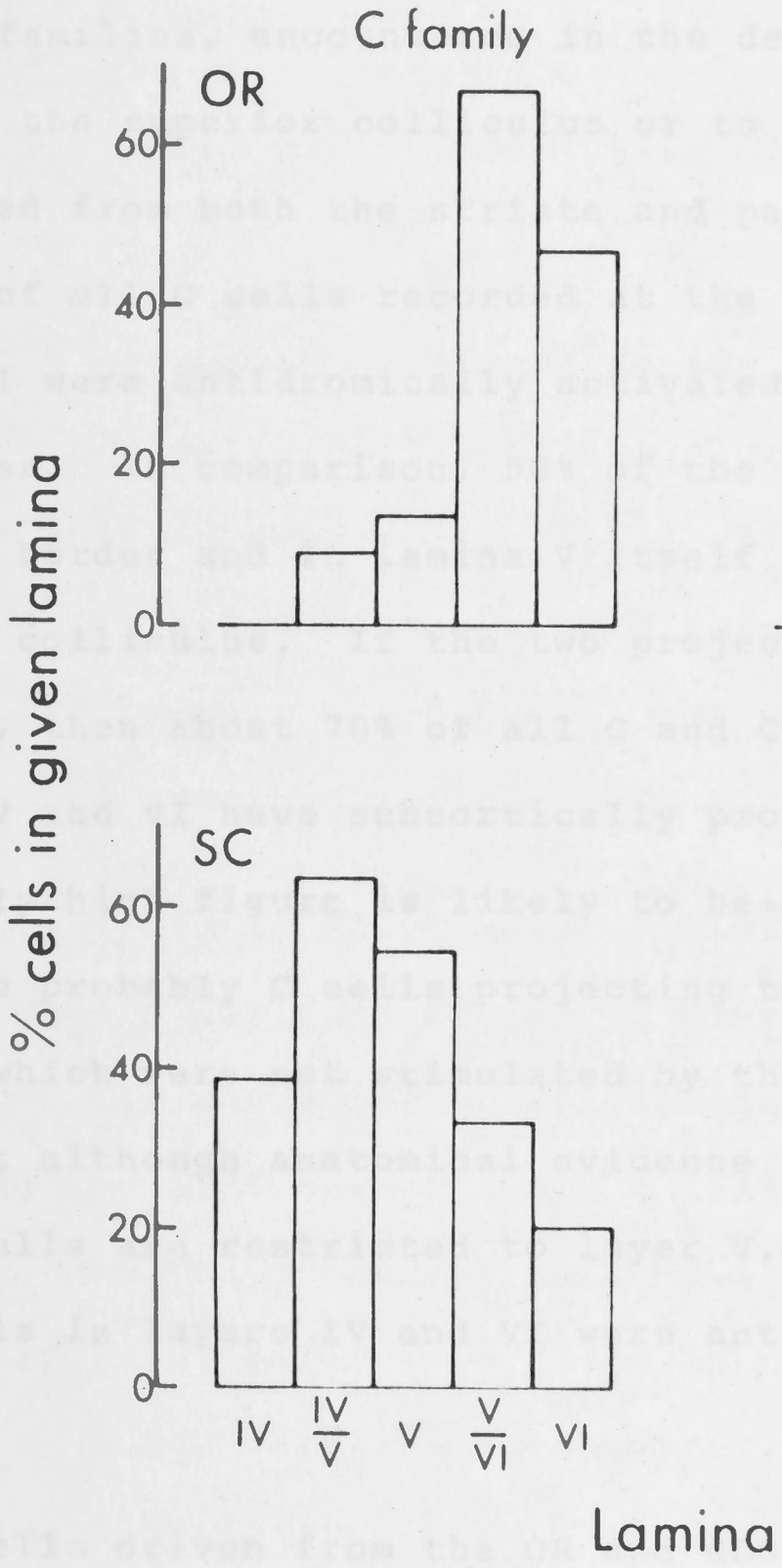


Fig. 16. Relative proportions of cells in the S and C families in each lamina which send axons to the superior colliculus or thalamus. Data pooled from areas 17 and 18. OR, corticothalamic neurons; SC, corticocollicular neurons.

Figure 16 shows the relative proportions of cells in the S and C families, encountered in the deeper laminae, which send axons to the superior colliculus or to the thalamus. The data are pooled from both the striate and parastriate cortex. Fifty percent of all C cells recorded at the V/VI border and in lamina VI were antidromically activated from the OR stimulating electrodes. In comparison, 58% of the C and C_H cells found at the IV/V border and in lamina V itself were efferent to the superior colliculus. If the two projections are considered together, then about 70% of all C and C_H cells encountered in laminae V and VI have subcortically projecting axons. This remarkably high figure is likely to be a lower limit since there are probably C cells projecting to other subcortical regions which were not stimulated by the SC and OR electrodes. Note that although anatomical evidence suggests that cortico-tectal cells are restricted to layer V, a significant proportion of C cells in layers IV and VI were antidromically driven from the SC.

S cells driven from the OR and dLGN electrodes are found exclusively below lamina V. Of the total number of S cells recorded in layer VI, 45% sent axons out of the cortex.

A comparison of the distribution and relative proportions of subcortically projecting neurons in areas 17 and 18 reveals striking similarities. Corticothalamic S cells comprise 43% and 55% of all lamina VI S cells recorded in the striate and parastriate cortex respectively. The distribution of cortico-tectal C and C_H cells in the two cortical regions is also very similar; 58% of all cells in the C family in laminae IV/V and V

of the striate cortex have corticocollicular axons compared with 50% of C and C_H cells in the parastriate cortex.

Cells not responsive to visual stimuli

A number of cells encountered in laminae IV to VI in area 17 and area 18 could not be placed in any of the receptive field groups. These cells fall into two categories; those that are very difficult to drive with visual stimuli (ND: not driven) and those that are responsive but have receptive field properties intermediate between S and C (NC: not classified). The numbers of each group recorded in layers IV to VI are shown in Table 3.

As described earlier, about 70% of C cells in lamina V and VI and 45% of S cells in lamina VI give rise to efferent fibres. In contrast, of the 42 ND cells recorded in these layers (including the IV/V border) only 8 (19%) were antidromically activated from the SC and/or OR. None of these visually non-drivable efferent cells were found in lamina IV of either cortical area and very few were orthodromically excited from the chiasm or radiation.

ND cells usually have no or very low spontaneous activity and by definition, fire only rarely when tested with visual stimuli. Many of these units were examined for half an hour or more but no stimulus was found which would elicit a consistent response. The correlation between visually and electrically non-drivable cells in area 18 has been described in Chapter 2 and the observation that only a few ND cells have efferent axons raises the possibility that they are interneurons.

TABLE 3

The number of not driven and not classified cells
in the deeper layers of the striate cortex

	AREA									
	17					18				
Lamina	IV	IV/V	V	V/VI	VI	IV	IV/V	V	V/VI	VI
Not driven	12	2	8	7	14	12	2	3	0	6
Not classified	4	1	1	1	3	1	1	0	0	0

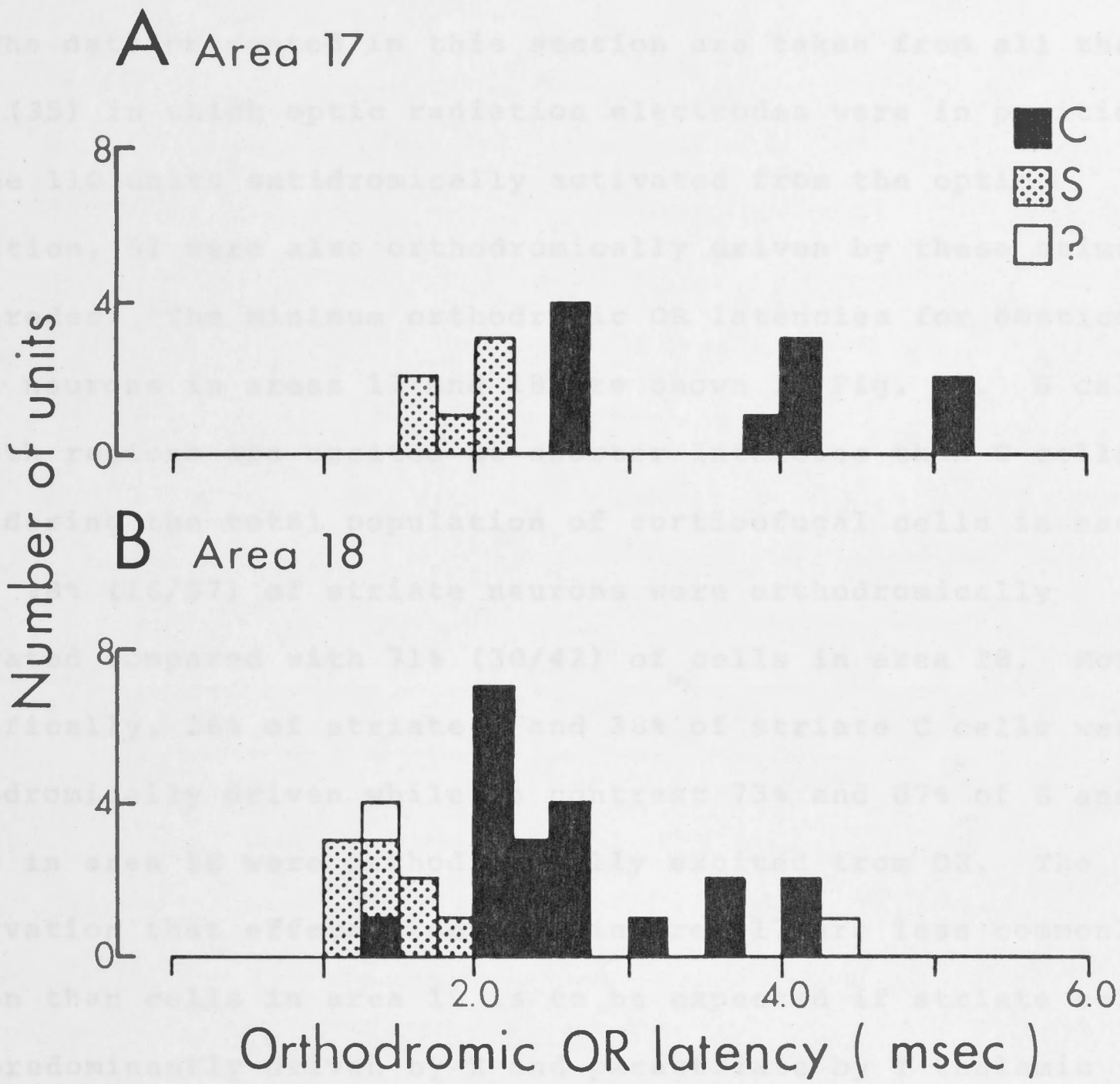


Fig. 17. Latencies of corticofugal cells orthodromically excited from the optic radiation (OR). Filled blocks, cells in the C family; dotted blocks, cells in the S family; open blocks, unclassified cells.

THE AFFERENT INPUT TO CORTICOFUGAL NEURONS

The data presented in this section are taken from all the cats (35) in which optic radiation electrodes were in position. Of the 110 units antidromically activated from the optic radiation, 51 were also orthodromically driven by these stimulating electrodes. The minimum orthodromic OR latencies for corticofugal neurons in areas 17 and 18 are shown in Fig. 17. S cells in both regions are excited at shorter latencies than C cells. Considering the total population of corticofugal cells in each area, 28% (16/57) of striate neurons were orthodromically activated compared with 71% (30/42) of cells in area 18. More specifically, 26% of striate S and 38% of striate C cells were orthodromically driven while in contrast 73% and 87% of S and C cells in area 18 were orthodromically excited from OR. The observation that efferent neurons in area 17 are less commonly driven than cells in area 18 is to be expected if striate cells are predominantly driven by X and parastriate by Y thalamic afferents (cf. Chapters 1 and 2).

The orthodromic latencies of S cells in area 17 (Fig. 17A) range from 1.6 to 2.2 msec. One of these efferent cells was also driven from the optic chiasm (OX) and the OX-OR difference was 1.8 msec which is indicative of a relatively slow (perhaps X) input to this neuron. The OR latencies of striate C cells on the other hand, ranged from 2.5 to 7.0 msec. These neurons are likely to be indirectly driven by thalamic afferents. Two of these neurons both had OX and OR latencies of 2.4 and 3.5 msec respectively which is suggestive of an indirect input by fast thalamic fibres (cf. Chapter 2). Many of the C cells in area 17

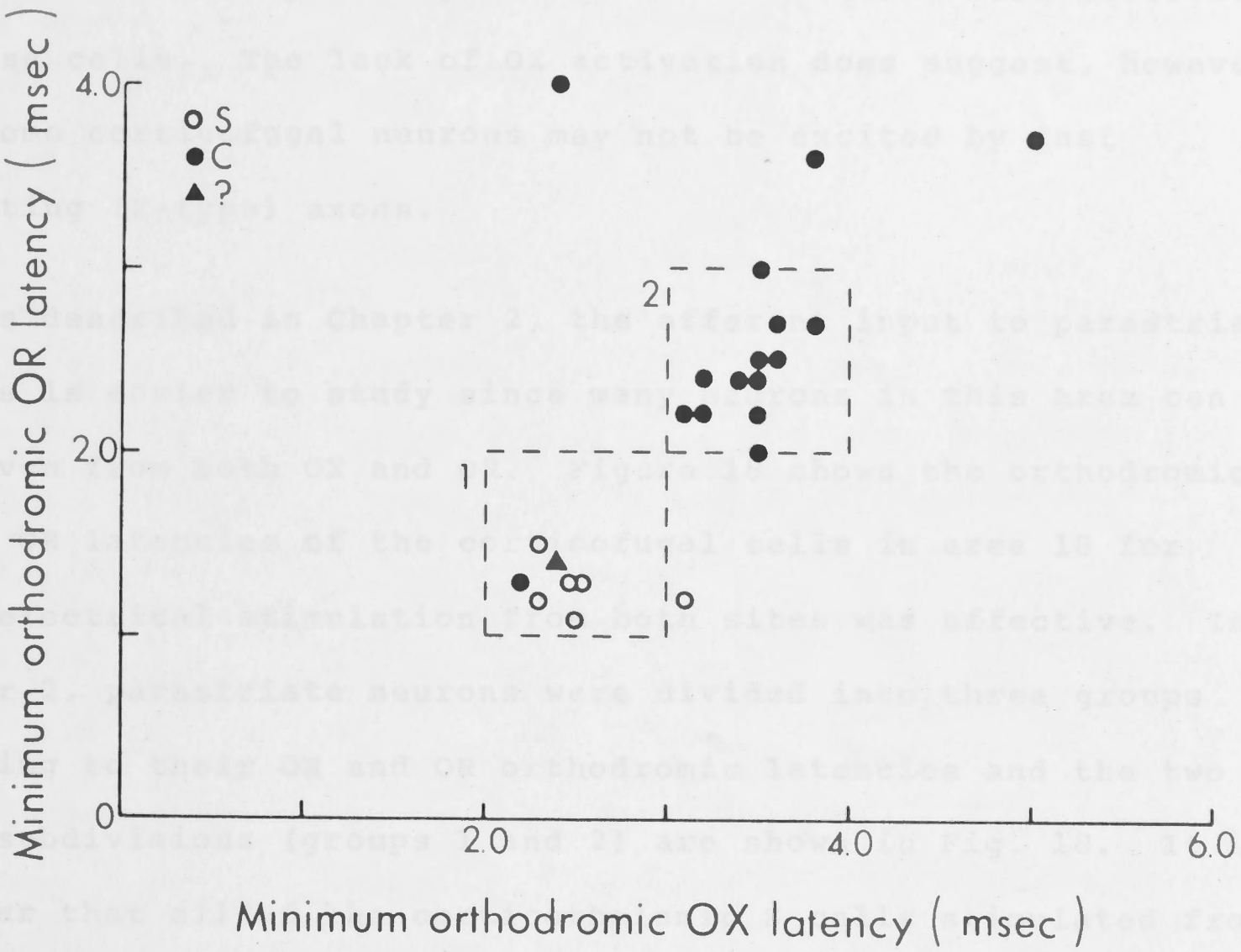


Fig. 18. Orthodromic optic chiasm (OX) and optic radiation (OR) latencies of corticofugal cells in area 18. Open circles, S cells; filled circles, C cells; filled triangles, unclassified cells. The boxes represent the orthodromic latency groups 1 and 2 as defined in Chapter 2. Group 1, monosynaptically excited cells; group 2, disynaptically excited cells.

could not be excited by chiasmal stimulation hence is was not possible to identify the type of thalamocortical fibre afferent to these cells. The lack of OX activation does suggest, however, that some corticofugal neurons may not be excited by fast conducting (Y-type) axons.

As described in Chapter 2, the afferent input to parastriate neurons is easier to study since many neurons in this area can be driven from both OX and OR. Figure 18 shows the orthodromic OX and OR latencies of the corticofugal cells in area 18 for which electrical stimulation from both sites was effective. In Chapter 2, parastriate neurons were divided into three groups according to their OX and OR orthodromic latencies and the two major subdivisions (groups 1 and 2) are shown in Fig. 18. It is clear that all of the corticothalamic S cells stimulated from both OX and OR are monosynaptically driven by fast thalamic afferents, while C cells with efferent axons are commonly indirectly excited. Twelve of these C cells have OX and OR latencies indicative of disynaptic activation by fast (Y-type) thalamic afferents. Four of the C cells in this group were antidromically activated from the SC.

The data presented in Fig. 18 indicates that lamina VI corticothalamic S cells in area 18 are monosynaptically driven by fast thalamocortical axons. C cells on the other hand, whether they project to the colliculus or the thalamus, are indirectly (most disynaptically) activated by incoming thalamic afferents. If, as suggested in Chapter 2, the intrinsic organization of areas 17 and 18 is very similar, it is highly probable that the same neural connectivity also holds for striate

corticofugal cells (Fig. 17A), with the proviso that many of these neurons may be activated (directly or indirectly) by more slowly conducting thalamocortical fibres.

DISCUSSION

Corticocollicular cells

In both the striate and parastriate cortex, all corticocollicular cells for which receptive fields can be plotted belong to the C family. These cells generally have a relatively high spontaneous discharge, are broadly tuned for stimulus orientation and respond to a wide range of stimulus velocities. Ninety-six percent of corticotectal neurons have binocular receptive fields and the majority are driven almost equally by the two eyes. The receptive fields of corticocollicular cells are relatively large when compared with the fields of other cells at corresponding eccentricities. Striate and parastriate cells which project to the SC are therefore very similar in their visual properties although some differences are apparent; area 18 corticotectal neurons have larger receptive fields than those in area 17 and also tend to respond to higher stimulus velocities. Collicular receptive fields increase in size in the deeper parts of the colliculus (Straschill and Hoffmann, 1969; Rosenquist and Palmer, 1971; Gordon, 1973). Whether this is related to the observation shown anatomically (Kawamura *et al.*, 1974; Updyke, 1977) and physiologically (McIlwain, 1977) that the corticotectal projection from area 18 projects slightly deeper than that from area 17 is not clear.

These results are substantially in agreement with previous reports (Palmer and Rosenquist, 1974; Singer *et al.*, 1975; Tretter *et al.*, 1975). However, Palmer and Rosenquist (1974) have reported that nearly all striate corticotectal cells do not show any summation with increasing stimulus length and

respond very well to small moving spots. In contrast, the present study has indicated that a number of corticocollicular C cells in both area 17 and 18 only respond well and consistently when longer stimuli are moved across the receptive field (Table 1). Many Palmer and Rosenquist type C cells are also found to project to the tectum, as are few C_H neurons. Although the majority of corticotectal neurons are direction selective, different types of C cell show different degrees of selectivity; cells responding to small spots are almost completely selective for the direction of movement, whereas cells which respond best to longer stimuli commonly show no or only weak selectivity. Kato, Bishop and Orban (1978) have shown that many striate C cells which, on first sight, resemble the Palmer and Rosenquist type of cell are in fact hypercomplex. Interestingly, their quantitative analysis indicates that many of these hypercomplex cells (hypercomplex II) are very direction selective whereas complex cells (equivalent to the C cells which respond best to long stimuli in this study) generally show no or only a little selectivity. The correspondence between the data of Kato *et al.* (1978) and the present results is immediately apparent, but since electrical stimulation was not attempted in their study it is not known what proportion of their complex and hypercomplex II cells have efferent axons. The two types of corticocollicular C cell also closely resemble the Type II and Type III complex cells of Sillito (1977a).

The majority of corticocollicular neurons give rise to fast conducting fibres and most of the information from the cortex reaches the colliculus in less than 3 msec (Fig. 12). The

mean SC latency for the 34 corticocollicular neurons is 2.6 msec which is very similar to the mean of 2.3 msec reported by both Palmer and Rosenquist (1974) and Toyama, Matsunami, Ohno and Tokashiki (1974) and of 2.8 msec reported by Hayashi (1969). The mean antidromic latencies of striate and parastriate corticocollicular cells are 2.4 and 3.1 msec respectively. This result is opposite to what one might expect from the study of McIlwain (1977) who found that the orthodromic latencies of tectal neurons after stimulation of area 18 were shorter than after area 17 activation.

Hoffmann (1973) has suggested that corticocollicular cells are monosynaptically driven by Y afferents from the dLGN. The results of the present analysis provide no support for this proposition (Figs. 17 and 18). In area 18 the data indicate that the majority of corticotectal cells are indirectly (most disynaptically) excited by fast conducting (Y) thalamocortical fibres. This result is substantially in agreement with that of Tretter *et al.* (1975). In area 17, no corticocollicular cells have orthodromic OR latencies less than 2.5 msec. These latencies are too long to be consistent with direct activation by Y geniculate cells (Chapter 2). Some striate cells efferent to the colliculus appear to be indirectly driven by fast fibres, however the majority are not activated from OX (in contrast to area 18) and this suggests that they may be innervated by more slowly conducting axons. In contrast, Singer *et al.* (1975) have reported that the striate corticotectal projection is mainly under the control of the Y system. However they do support the observation that the majority of these efferent cells are

are indirectly excited by thalamic afferents.

HRP studies described in the present study (Fig. 2) and carried out by other workers (Hollander, 1974; Gilbert and Kelly, 1975; Magalhäes-Castro *et al.*, 1975; Baleydier, 1977) indicate that corticocollicular neurons are restricted to lamina V of both the striate and parastriate cortex. Consistent with this observation, the majority of antidromically activated cortico-tectal cells are located at the IV/V border and in lamina V (Fig. 9). However, occasional corticocollicular cells are found in more superficial and deeper layers. Figure 16 shows that 38.5% and 20.0% of all cells in the C family in layers IV and VI respectively are efferent to the colliculus. Since the somata of corticotectal neurons are in layer V, this result suggests that on a number of occasions the microelectrode was recording from parts of the neuron distal to the cell body. HRP studies show that the large pyramids in layer V are always labelled after an SC injection. Further, the short antidromic latencies of corticotectal neurons suggest that their axons and presumably their cell bodies are large. Since the smaller, long latency corticothalamic cells are never encountered outside layer VI (see below), it would appear that recording at a site away from the soma only occurs when the larger cells in the cortex are involved. Both the apical dendrites and axons of these layer V pyramidal cells are large and it is not clear which of these structures is the site of this 'extra-somal' recording. The observation that 40% of all the C cells ostensibly recorded in lamina IV are in fact in lamina V indicates that the proportion of genuine layer IV C cells is much lower than it appears (Chapter 1, Chapter 2). Similarly, the number of C cells in

layer V itself is likely to be higher than previous estimates have indicated.

Corticothalamic cells

It has already been pointed out that one of the major difficulties of electrical stimulation is in determining whether axon terminals or fibres of passage are being activated. Evidence has been presented which indicates that the corticofugal fibres excited from the OR electrodes but not activated from the SC are projecting to the thalamus and are not passing on to other subcortical sites. This conclusion is based primarily on the observation that the majority of these efferent cells are found in layer VI, the lamina of origin of the corticogeniculate pathway. It is now necessary to consider this proposition in more detail.

Efferent S cells

Considering the efferent S cell population, the observation that all of these cells are located in laminae V/VI and VI and are commonly activated from the anterior OR stimulating electrodes placed near or more usually just within the dLGN clearly suggests that these corticofugal cells are projecting to the geniculate complex. Further, the observation that the axons of efferent S cells are slowly conducting and therefore of small diameter is consistent with anatomical evidence that the corticogeniculate projection contains many fine fibres (Guillery, 1967; Niimi *et al.*, 1971; Kawamura *et al.*, 1974). Guillery (1967) has suggested that the fine degenerating axons seen in the dLGN after cortical lesions may be collaterals of coarser fibres.

However, the data in Fig. 14 clearly shows that the small corticogeniculate fibres conduct slowly along their entire length and are independent of the fast corticofugal system.

Corroborative evidence that S cells are efferent to the dLGN comes from studies which have examined the responses of geniculate neurons after electrical stimulation of the visual cortex. Cleland, Levick, Morstyn and Wagner (1976) and Dubin and Cleland (1977) report that some cells recorded within the main laminae of the dLGN and in the perigeniculate nucleus (a layer of cells which lies just above lamina A of the dLGN) are activated transsynaptically after cortical stimulation. Both types of cell have been identified as interneurons by Dubin and Cleland (1977). The orthodromic latencies of perigeniculate interneurons are characteristically faster than those of cells recorded within the dLGN (intrageniculate interneurons). Adding together the data of Cleland *et al.* (1976) and Dubin and Cleland (1977), perigeniculate interneurons have orthodromic latencies between 0.9 and 3.0 msec while intrageniculate interneurons are activated at latencies which range from 3.0 to 9.0 msec. In comparison, the antidromic latencies of corticofugal S cells range from 1.5 to 29.0 msec. Given that the transmission delay across a synapse is about 0.8 msec (Chapter 2), then only 20% of efferent S cells have axons which conduct fast enough to account for the orthodromic latencies of perigeniculate neurons. Indeed, all of the 19 orthodromically activated perigeniculate neurons described by Dubin and Cleland (1977) had latencies less than 1.9 msec. Only one, at most, of the S cells in the present study could possibly be efferent to these interneurons. On the other hand, the correlation between the orthodromic latencies of

intrageniculate interneurons and the antidromic latencies of layer VI S cells strongly suggests that these cortical cells provide much of the input to the neurons within the dLGN.

Efferent C cells

A number of efferent C cells with fast conducting axons are antidromically excited from the OR and/or dLGN stimulating electrodes but are not driven from the SC. The majority of these neurons are located in lamina VI and may also be efferent to the geniculate. However, it should be stressed that unlike S cells, the laminar position of corticofugal C cells does not give an unambiguous indication as to the destination of their axons; long latency S cells activated from the dLGN stimulating electrodes are all found at the V/VI border and in layer VI itself whereas fast conducting corticocollicular C cells are not necessarily restricted to layer V (see above). As suggested earlier therefore, it would seem that the larger the cell, the greater the likelihood of recording from a site distal to the cell body. Since corticothalamic C cells are also fast conducting, it is possible that some of these lamina VI neurons may in reality have their cell bodies in layer V. Similarly, the few efferent C cells in layer V which apparently do not project to the colliculus may be in layer VI. Considerations such as these make it difficult to use the laminar position of efferent C cells as a guide to assessing the destination of their axons.

However, the probability of recording at a point distant from the soma is likely to be very similar in fast conducting C

cells which do or do not project to the tectum. Since the effect of this 'extra-somal' recording is likely to blur rather than substantially alter the laminar distribution of a given efferent class, the difference in the proportions of corticocollicular and corticothalamic neurons in the various laminae is still significant (Fig. 16). Clearly, cells driven from the colliculus are most common in lamina V whereas other efferent C cells are concentrated in lamina VI.

If these layer VI C cells are indeed efferent to the geniculate, where do they project? The antidromic latencies of layer VI C cells not efferent to the tectum range from 0.5 to 1.5 msec. These latencies appear to be too short to account for the input to intrageniculate interneurons (see above) unless one postulates the existence of complicated polysynaptic circuits, or suggests that recruitment of a number of fast conducting fibres are necessary to produce a suprathreshold excitatory postsynaptic potential. Since the intrageniculate interneurons appear to be involved in precise, spatially organised inhibition (see below), such a diffuse innervation by large field C cells seems unlikely. Rather, from the similarity in the orthodromic latencies of perigeniculate interneurons and the antidromic latencies of layer VI C cells, it is quite possible that many of these fast conducting corticofugal cells innervate the perigeniculate nucleus. That the visual cortex projects to the perigeniculate nucleus has been shown in a number of anatomical studies (Kawamura *et al.*, 1974; Updyke, 1975, 1977). Furthermore, the studies of Guillery (1967) suggest that degenerating fibres found just above lamina A are coarser than those within the dLGN

itself (see for example his Fig. 3, p. 203). The lamina of origin of cortico-perigeniculate fibres is not known, but it is quite likely to be layer VI; HRP injections into the dLGN must sometimes spread into this nucleus, yet labelled cells outside lamina VI are never or only rarely encountered.

Dubin and Cleland (1977) provide evidence that perigeniculate interneurons are excited by axon collaterals of brisk transient relay cells and suggest that orthodromic activation of these interneurons after visual cortex stimulation is mediated by these collateral fibres. However, corticofugal fibres terminating in this nucleus would undoubtedly be activated by the stimulating electrodes adjacent or within the dLGN employed in the present study. An alternative or additional input to perigeniculate interneurons is therefore suggested by the present results.

The small number of corticofugal C cells in laminae IV/V and V which do not project to the tectum (it should be pointed out that lack of collicular activation does not *necessarily* mean the cell is not efferent to this region) may be displaced layer VI cells or may be projecting to thalamic regions other than the dLGN and the perigeniculate nucleus. It is possible for example, that they are efferent to the lateral posterior nucleus (Lund, Henry, Macqueen and Harvey, in preparation). If one assumes that at least some of the corticothalamic cells are in layer V, it is perhaps surprising that the projection to the nuclei medial to the dLGN is so sparse. It may be that many lamina V cortico-collicular cells branch and send axon collaterals to these thalamic regions (cf. Guillery, 1967). Albus and Donate-Oliver (1977) have reported that C cells in layer V also project to the pons.

However, it is unlikely that the layer V C cells described in the present study project to this region since all of these cells had receptive fields within 5^{o} of the area centralis and Albus and Donate-Oliver (1977) have shown that corticopontine cells are only detected in peripheral parts of the visual field representation.

As yet, it is not clear what lamina is involved in the cortical projection to the medial interlaminar nucleus (MIN) and ventral lateral geniculate nucleus. Using the arguments applied earlier to the perigeniculate projections, it is quite likely that the projection to MIN, at least, originates from cells in layer VI. Niimi *et al.* (1971) and Kawamura *et al.* (1974) have reported that area 18, but not area 17, sends fibres to MIN. Furthermore, Kawamura *et al.* (1974) and Updyke (1975) indicate that area 18 projects heavily onto lamina C of the dLGN whereas area 17 projects more uniformly to all layers. Since lamina C and MIN send many afferents to area 18 (Hollander and Vanegas, 1977; LeVay and Ferster, 1977) it is possible that the parastriate cortex may be involved in a specific recurrent pathway which is distinct from the area 17 system.

In summary, there appear to be at least three corticothalamic pathways. It is suggested that lamina VI S and C cells provide much of the input to intrageniculate and perigeniculate neurons respectively, while C cells in lamina V are efferent to nuclei medial to the dLGN such as the lateral posterior nucleus.

The concept of more than one efferent system to the dLGN receives support from a number of studies. Singer *et al.* (1975)

and Tretter *et al.* (1975) have reported that both simple and complex cells in the striate and parastriate cortex project to the dLGN. Further, Singer *et al.* (1975) note that complex cells tend to have faster conducting subcortical axons than other cell types. Their mean antidromic dLGN latencies for complex cells was 1.2 msec compared to 2.7 msec for simple cells. These results are therefore similar to those described in the present analysis. Compared to Singer *et al.* (1975) however, the mean antidromic latency of striate S cells is longer (6.3 msec) and the proportion of corticogeniculate S cells is higher.

Gilbert (1977) has also shown that simple and complex cells are efferent to the dLGN. He reports that 80% of corticogeniculate neurons in layer VI of area 17 have complex receptive fields. In contrast, the present study indicates that 73% of all layer VI corticothalamic neurons are S cells. This discrepancy could be due both to difference in receptive field classification and to sampling bias resulting from the use of different microelectrodes. As described in Chapter 1, a number of Gilbert's standard complex cells may in fact be simple cells which might account for some of the discrepancy described above. In addition however, the antidromic latencies found by Gilbert (1977) ranged from 1.1 to 3.2 msec, whereas 63% of the cells in the present study had latencies longer than 3.2 msec. Thus, irrespective of how the units were classified, over half of the corticogeniculate cells in the present study appear to be unrepresented in Gilbert's sample. All of these long latency units were classed as S cells and it has already been suggested that their soma are small. It is therefore possible that the

frequency with which these small cells are encountered may vary with the type of microelectrode (cf. Harvey, 1978). It should also be pointed out that Gilbert did not have stimulating electrodes in the SC. Since the majority of corticotectal cells are also stimulated from the OR and since these cells are occasionally found in layer VI (Fig. 9, Fig. 16) it is possible that some of Gilbert's efferent complex cells are projecting to the SC rather than the dLGN.

With regard to the afferent connections of corticothalamic neurons, the orthodromic OX and OR latencies of corticogeniculate S cells in area 18 indicate that most of these neurons are monosynaptically excited by fast thalamic afferents. In contrast, corticothalamic C cells in area 18 are commonly indirectly activated by these thalamocortical fibres. The present results are therefore similar to those of Tretter *et al.* (1975). The data are less clear in area 17 since it was not possible to elicit consistent OR or OX activation in striate cells. However, all of the striate corticofugal S cells which were driven from OR had latencies less than 2.0 msec. These cells are likely to be directly innervated by thalamic afferents. One cell had OX-OR latencies indicative of a relatively slowly conducting input, however, the general lack of OX excitation makes it impossible to be certain about the type of fibre innervating most cortico-geniculate S cells in area 17. In this regard, Singer *et al.* (1975) have suggested that corticothalamic cells may be either X or Y driven although it is not clear from their data what proportion of efferent simple and complex cells receive X and Y axons respectively. From the present results, corticothalamic

C cells in area 17 have longer OR latencies and as with C cells projecting to the colliculus, it is unlikely that they are monosynaptically excited by thalamic fibres. Contrary to area 18, where activation from OX was common, the lack of OX stimulation in the majority of striate corticofugal cells suggests that they may be innervated by more slowly conducting geniculate afferents.

Functional considerations

Corticocollicular projection

The majority of cells recorded in the superficial layers of the superior colliculus are binocular, direction selective, responsive to moving rather than stationary stimuli and have inhibitory regions surrounding the excitatory discharge area (McIlwain and Buser, 1968; Sterling and Wickelgren, 1969; Rosenquist and Palmer, 1971; Mize and Murphy, 1976). Although there is some disagreement as to what extent the responses of collicular neurons are altered after lesions in the visual cortex, most reports indicate that after removal of the cortex, collicular cells become less direction selective and less binocular, more neurons being driven by the contralateral eye (Wickelgren and Sterling, 1969; Rizzolatti *et al.*, 1970; Rosenquist and Palmer, 1971; Mize and Murphy, 1976). Rizzolatti *et al.* (1970) and Mize and Murphy (1976) also suggest that this effect is more pronounced in the superficial as opposed to the deeper layers of the SC. The degree of alteration in the response properties of collicular cells appears to depend on what visual cortical areas are removed. Both Rosenquist and Palmer (1971) and Mize and Murphy (1976) show that destruction of area 17 alone

is sufficient to cause the effects described above. Further, large cortical lesions which spare area 17 have no effect on the responses of neurons in the SC (Rosenquist and Palmer, 1971) and these authors conclude that the direction selectivity and binocularity displayed by collicular cells is dependent solely on the integrity of the striate cortex. The influence of more lateral visual areas is therefore unresolved. That they are afferent to tectal neurons has been shown physiologically by McIlwain (1977), who reports that many individual collicular cells receive convergent excitatory inputs from retinotopically related regions in areas 17, 18 and 19.

How significant are the cortically dependent response properties of collicular neurons in terms of the functional importance of the SC as a whole? Although the role of the superior colliculus is still the subject of much speculation, the tectum does appear to be involved in certain aspects of visual attention and perception and in the control of head and eye movements. Evidence that the colliculus is concerned with these behaviours comes from a number of studies. Electrical stimulation of the colliculus produces conjugate and contraversive eye saccades as well as head movements (Syka and Radil-Weiss, 1971; Straschill and Rieger, 1973; Roucoux and Crommelinck, 1976; Stein, Goldberg and Clamann, 1976). Further, Norton (1974) has shown that the development of two visually guided behaviours in kittens is correlated with the maturation of SC receptive field properties. The two behaviours are the orienting of the animal to a stimulus presented in the visual field and the following of a stimulus moved through the field. Finally, after

unilateral collicular lesions, cats neglect stimuli presented in the contralateral visual field and suffer motor deficits in eye, head and body movements (Sprague and Meikle, 1965).

However, despite the observation that some of the response properties of collicular neurons are dependent on an input from area 17, removal of areas 17 and 18 does not alter the visuomotor behaviour of cats (Sprague, Levy, DiBerardino and Berlucchi, 1977). Eye and head movements as well as fixation appear normal. On the other hand, destruction of all visual areas *except* areas 17 and 18 has much more obvious effects. Animals cannot follow moving stimuli for more than a short distance, their depth judgement is poor and their behavioural responses to visual stimuli are generally slow.

The role of the corticocollicular projection from areas 17 and 18 is thus something of a mystery. The present results indicate that the cells afferent to the colliculus are C cells in both the striate (cf. Palmer and Rosenquist, 1974) and parastriate cortex. Corticocollicular cells are almost always binocular and many are direction selective, the major difference between area 17 and 18 neurons being the size of the receptive fields. In general, the receptive fields of corticotectal neurons are large and the cells are responsive to a large range of stimulus velocities. Thus whatever the exact role of the corticocollicular system, the information transmitted from the cortex appears to be related to the movement and general location of a visual stimulus rather than to fine details about the form and texture of the object. Further, the fact that corticocollicular cells are invariably fast conducting suggests,

perhaps, that the system is involved in dynamic rather than static visual behaviours.

It may be that the behavioural tests used to examine the effects of occipital lesions (Sprague *et al.*, 1977) are not sensitive enough to recognise deficits resulting from the loss of these areas. It is also possible that the cells in the superficial layers of the SC which are apparently most influenced by areas 17 and 18 are not themselves directly involved in the control of eye movements and visual orienting but are concerned with some other behavioural task. Such a situation has been shown to occur in the tree shrew. Animals with lesions restricted to the superficial layers (which receive the cortical input) suffer deficiencies in form discrimination but are normal in their visually guided behaviour, whereas animals with large collicular lesions also show distinct deficiencies in their ability to orient towards or track a visual stimulus (Casagrande, Harting, Hall, Diamond and Martin, 1972; Casagrande and Diamond, 1974). These reports relate the above observations to the fact that the superficial layers of the SC project to the visual thalamus while deeper layers are efferent to non-visual thalamic regions and to the brain stem motor area.

A similar distribution of efferent projections within the SC has recently been described in the cat (Graham, 1977). The superficial layers project to nuclei in the pretectum and thalamus that are specifically involved in visual processing, while deeper layers project to nuclei in the reticular formation, to some precerebellar nuclei, to the spinal cord and to several non-visual areas in the thalamus and midbrain. Although

behavoural studies similar to those in the tree shrew (see above) have not been reported, physiological investigations reveal that receptive fields of cells in the superficial layers of the cat SC are small and exclusively visual whereas cells deeper in the colliculus have more diffuse visual receptive fields and respond to topographically related auditory and somatosensory stimuli as well (Gordon, 1973; Stein, Maghalhães-Castro and Kruger, 1976). Stein *et al.*(1976) suggest that visual, somatic, and acoustic cells "converge on a common delivery or distribution system, which is located in the intermediate-deeper SC strata and organizes orienting and following responses on the basis of multimodality cues". In other words, the apparent absence of behavioural changes in cats with lesions in areas 17 and 18 (Sprague *et al.*, 1977) may arise because the functional integrity of the deeper collicular layers largely remains unaffected (Rizzolatti *et al.*, 1970; Mize and Murphy, 1976). These regions are apparently intimately concerned with attention and motor functions and so gross behavioural responses will appear normal. The loss of direction selectivity and binocularity in superficial SC neurons after cortical lesions is likely to manifest itself in more subtle ways which have yet to be recognised.

Corticothalamic projection

It has been suggested that there may be at least three subgroups within the population of corticothalamic cells. Layer V C cells project to thalamic nuclei medial to the dLGN (the same cells may also send axons to the tectum), layer VI C cells project to the perigeniculate nucleus and layer VI S

cells provide the cortical input to the intrageniculate interneurons of the dLGN. These pathways have been derived from (1) the lamina of origin of corticofugal cells (2) the observation that the majority of cells not activated from the SC are excited by dLGN stimulation and (3) a comparison of the antidromic latencies of corticothalamic cells with the orthodromic latencies of perigeniculate and intrageniculate interneurons.

The two types of interneuron described by Dubin and Cleland (1977) differ markedly in their visual responses and in their connectivity. Intrageniculate interneurons, found within the main laminae of the dLGN are very similar to relay cells in that they have concentrically organised receptive fields and receive their major excitatory input from a few retinal afferents of the brisk or sluggish, sustained or transient type. The major difference between these neurons and relay cells is that they do not project to the visual cortex but are activated transynaptically at relatively long latency after cortical stimulation. The other type of interneuron, encountered in the perigeniculate has a large receptive field, is generally binocularly innervated, gives ON/OFF responses throughout its receptive field and responds well to fast velocities. Perigeniculate cells are activated at short latencies after stimulation of the visual cortex. There is some uncertainty whether this excitation is of cortical origin or arises from activation of recurrent collaterals of relay cells within the dLGN. However, as described earlier, a neural substrate does exist for feedback from cortex since the

perigeniculate receives a projection from area 17 and area 18 (Kawamura *et al.*, 1974; Updyke, 1977). A recent review (Singer, 1977) has summarised the various types of inhibitory interactions encountered in the dLGN. From an analysis of the physiological properties of the two types of interneuron, it has been suggested that intrageniculate interneurons are involved in precise, retinotopically organised inhibitory pathways and that the perigeniculate interneurons are concerned with more global, diffuse inhibitory interactions which non-specifically modulate the excitability of dLGN neurons (Dubin and Cleland, 1977; Singer, 1977).

The proposal that S and C cells project to intrageniculate and perigeniculate interneurons respectively is especially significant when considered in the light of the suggestions discussed above. Corticothalamic C cells are generally binocular, have large receptive fields and respond to a wide range of stimulus velocities. These neurons are therefore likely to be concerned with the movement and general location of a visual stimulus rather than in specific details about its form and spatial position. Furthermore, impulses initiated in cortico-thalamic C cells reach the thalamus in less than 2 msec. This fast C cell system is just the sort of pathway one might expect to be afferent to a diffuse non-specific inhibitory system which is involved in the global modulation of geniculate alertness and arousal.

S cells on the other hand, especially in area 17, have small receptive fields, are almost always direction selective and commonly respond optimally to more slowly moving stimuli. S cells

are therefore very specific in their stimulus requirements and there would be a great deal of redundancy if such cells were afferent to a diffuse inhibitory network. They are far more likely to project onto the precise, retinotopically organised inhibitory pathways which involve the intrageniculate neurons.

Sanderson, Bishop and Darian-Smith (1971) and Schmielau and Singer (1977) have examined the effects of cortical removal and cooling on binocular interactions in the dLGN. Although neurons in the dLGN appear to be monocular, binocular presentation of visual stimuli often reveals a subliminal input from the corresponding point in the non-dominant eye (Singer, 1970; Sanderson *et al.*, 1971). Sanderson *et al.* (1971) found that most of the receptive fields in the non-dominant eye were purely inhibitory and reported that this inhibition was fairly weak. Removal of the visual cortex had no effect on these inhibitory interactions.

In the study of Schmielau and Singer (1977), 75% of neurons recorded in laminae A and A_1 of the dLGN showed binocular interactions. In a few cells, the input from the non-dominant eye was purely inhibitory and in the remainder facilitatory or inhibitory effects were seen depending on the site of stimulation within the non-dominant eye. After cooling of the visual cortex, facilitatory interactions were completely abolished and binocular inhibition was reduced. It was suggested that facilitation is dependent on corticofugal pathways, while inhibition also depends on intrageniculate networks (cf. Sanderson *et al.* 1971).

These results have been incorporated into a model which describes how the visual cortex might control binocular

interactions in the dLGN (Schmielau and Singer, 1977; Singer, 1977). In essence, it is proposed that disparity sensitive cells in the visual cortex which are optimally excited by an appropriate stimulus presented to the two eyes facilitate the transmission of signals through the dLGN by suppressing binocular inhibition in the corresponding projection column as well as by facilitating the cells within this column. Cells for which the binocular images are non-optimal would be inhibited (Barlow, Blakemore and Pettigrew, 1967; Pettigrew, Nikara and Bishop, 1968; Bishop, Henry and Smith, 1971) and intrinsic inhibitory interactions within those projection columns would predominate. As a result the corticofugal control of binocular interactions in the LGN "is selectively facilitating the transmission of signals from binocularly viewed objects that are near the fixation plane and can be fused to one image. Signals from objects before or behind the fixation plane, which cannot be fused and therefore give rise to double images, remain subject to binocular inhibition in the LGN" (Singer, 1977).

Obviously, if the visual cortex is to play such a role, the cells feeding back to the geniculate must themselves be sensitive to the relative positions of binocularly viewed stimuli. The suggestion from the present study, that S cells provide the input to intrageniculate neurons, is very relevant in this context. Although only about half of the corticogeniculate S cells are binocular, it is probable that most if not all S cells in the striate cortex are binocularly influenced, the input from the non-dominant eye being subliminal (either excitatory or inhibitory) and only seen when the cell is activated simultaneously from the two eyes (Bishop *et al.*, 1971; Kato, Bishop and Orban, in

preparation). S cells in area 17 are finely tuned to binocular spatial disparity (Barlow *et al.*, 1967; Pettigrew *et al.*, 1968; Bishop *et al.*, 1971; Nelson, Kato and Bishop, 1977) and thus appear to be capable of encoding exactly those features of the stimulus which are necessary for the corticofugal control of binocular interactions in the dLGN. A quantitative analysis of the binocular properties of efferent as opposed to non-efferent S cells in the striate and parastriate cortex is now required in order to test this possibility.

Given the apparent specificity of the corticogeniculate projection, one may ask why removal of the cortex does not produce more profound changes in the response properties of dLGN cells. It is possible that effects would be more noticeable in intrageniculate interneurons rather than relay cells. Since interneurons are recorded only rarely (e.g. Dubin and Cleland, 1977) it is likely that most of the geniculate cells studied before and after cortical cooling or ablation are relay cells. Secondly, none of the studies which have investigated the influence of the corticogeniculate pathway have used stimuli appropriate for the visual cortex. Schmielau and Singer (1977), for example, used spots of light, a stimulus which is by no means optimal for S cells in area 17. Therefore even with an intact cortex, the corticogeniculate system will not be exerting its maximum effect.

Conclusions

In summary, the present results indicate that C cells in both areas 17 and 18 project to the superior colliculus, the perigeniculate nucleus and perhaps the lateral posterior nucleus.

All of these pathways are fast conducting and their influence appears to be related to general alerting and attention mechanisms. Although the exact nature of the cortical influence on tectal neurons is not yet clear, it is likely to be concerned in some way with behaviours such as foveation and the orienting responses associated with eye movements. In contrast the S cell projection to the dLGN may be involved in more static visuomotor behaviours which arise during fixation; corticofugal control improves the contrast between objects, in, as opposed to away from, the fixation plane and is perhaps important in keeping the eyes locked onto a target which is of particular interest to the animal. One might speculate that this system can only operate once the appropriate orienting responses have being made towards the stimulus of interest. It is perhaps significant, therefore, that S cells have much more slowly conducting efferent axons than C cells.

Finally, it is clear that the efferent projections of area 17 and area 18 are very similar. C cells in both areas project to the SC and perhaps the perigeniculate and lateral posterior nucleus of the thalamus,whereas layer VI S cells appear to innervate neurons within the dLGN. As described in Chapter 2, this similarity in the extrinsic connections of the striate and parastriate cortex suggests that both areas are concerned with dynamic and static visuomotor behaviours. A separation of form perception in area 17 and motion perception in area 18 (Orban, 1977) is therefore not supported by these results.

CHAPTER FOUR

CONNECTIONS BETWEEN AREA 17 AND THE CLARE-BISHOP CORTEX

INTRODUCTION

The final two chapters of this thesis describe physiological experiments which have examined some aspects of the corticocortical connections of the cat visual cortex. Studies of this nature help define the type of information being transmitted from one visual area to another and provide clues as to how the various regions interact with each other. In this section the interrelationship between area 17 and the Clare-Bishop area (lateral suprasylvian cortex) is considered.

A number of studies have shown that the lateral suprasylvian cortex is involved in the processing of visual information (Clare and Bishop, 1954; Hubel and Wiesel, 1969; Wright, 1969; Rizzolatti and Camarda, 1975; Spear and Baumann, 1975a; Camarda and Rizzolatti, 1976b; Palmer, Rosenquist and Tusa, 1978). The visual input to this region is mediated by both thalamic and corticocortical afferents. Although originally thought to receive afferents from the dorsal lateral geniculate nucleus (Glickstein, King, Miller and Berkley, 1967; Wilson and Cragg, 1967; Niimi and Sprague, 1970; Burrows and Hayhow, 1971) it is now generally agreed that the major thalamic input to the Clare-Bishop area (CB) arises from the lateral nuclear-pulvinar complex which lies medial to the lateral geniculate nucleus (Heath and Jones, 1970,1972; Graybiel, 1972; Rosenquist, Edwards and Palmer, 1974; Gilbert and Kelly, 1975). With regard to the cortical connections, the Clare-Bishop cortex receives visual association fibres from a number of areas in both the ipsilateral and contralateral

hemisphere (Hubel and Wiesel, 1965; Garey, Jones and Powell, 1968; Wilson, 1968; Heath and Jones, 1970, 1972; Kawamura, 1973; Maciewicz, 1974; Gilbert and Kelly, 1975).

Of particular relevance to the present study is the relationship between area 17 and the Clare-Bishop cortex. Degeneration and autoradiographic studies indicate that there is an ipsilateral topographic projection from the striate cortex to the lateral suprasylvian area (Hubel and Wiesel, 1965; Wilson, 1968; Heath and Jones, 1970; 1972; Kawamura, 1973) as well as a reciprocal pathway from the Clare-Bishop cortex back to area 17 (Heath and Jones 1970, 1972). Using the technique of retrograde transport of horseradish peroxidase (HRP) it has been shown that almost all of the projection from area 17 arises from pyramidal cells in laminae II and III (Maciewicz, 1974; Gilbert and Kelly, 1975). Gilbert and Kelly, (1975) report that these cells are totally confined to layers II and III whereas Maciewicz (1974) indicates that labelled cells are occasionally found in the deeper layers.

After unilateral lesions of areas 17, 18 and 19, neurons in the ipsilateral Clare-Bishop cortex become less direction selective and more monocular (Spear and Baumann, 1975b). However, many of the receptive field properties of lateral suprasylvian cells are not affected by visual cortex lesions which suggests that much of the visual processing in the Clare-Bishop area is dependent on the integrity of the thalamic rather than the cortical pathways. Elucidation of the type of information being transmitted to the Clare-Bishop cortex from area 17 will, nonetheless, give indications as to the exact

nature of the striate influence on this area. The primary aim of the present study is therefore to separate, through physiological identification, those striate cells sending axons to the Clare-Bishop cortex.

METHODS

The general experimental procedures employed in this study have been described earlier (Chapter 1). In 14 cats, single cell activity in the striate cortex was monitored using tungsten in glass microelectrodes. With stimulating electrodes in the medial bank of the lateral suprasylvian sulcus it was possible to determine if the striate neuron could be driven antidromically or orthodromically from CB. Spike collision, fixed latency of response and the following of high frequency stimulation were adopted as criteria for antidromic activation (Chapter 3).

Craniotomies were performed for the insertion of the recording electrode in the striate cortex, for a line of 6 stimulating electrodes (each 2 mm apart) angled into the Clare-Bishop area (from HC coordinates, AP-2 to +10 and ML 14) and for a pair of stimulating electrodes placed in the optic radiation (cf. Chapter 1). The electrodes in the optic radiation (OR) were used to confirm that the electrodes in the Clare-Bishop cortex were specifically activating that area rather than the underlying white matter (see RESULTS). Generally, the recording electrode entered the striate cortex close to the HC coordinates, AP-2; ML 1.5. To extend the traverse of laminae II and III, the electrode was tilted so that its tip was angled forward 30^{o} and medially 10^{o}. As for all experiments, Nissl-stained sections(40 µm in thickness) were prepared for the reconstruction of the electrode path and relative depths in each track were assessed from

electrolytic lesions spaced at intervals of approximately 1 mm. Only those tracks in which lesions were unambiguously defined are included in the analysis. The laminar pattern in the Nissl preparations was identified by using criteria closely conforming to those of O'Leary (1941) (cf. Chapter 1). Histological checks were also carried out in order to verify that the Clare-Bishop stimulating electrodes were correctly positioned in the lateral suprasylvian cortex. Since stimulation of the underlying white matter would complicate the analysis, the stimulating electrodes were rarely driven deep into the lateral suprasylvian area.

RESULTS

General Comments

In 24 electrode penetrations, the laminar position of 311 striate units were unambiguously determined. Of these units, 211 were classed according to their responses to both moving and stationary visual stimuli. The classificatory procedures and the nomenclature used in these experiments have been described in detail in Chapter 1. Eleven cells were antidromically activated from the Clare-Bishop area and a further 52 were orthodromically excited from this site.

Cells efferent to the Clare-Bishop area

All of the neurons antidromically activated from the ipsilateral lateral suprasylvian cortex were located above lamina IV. Eight of these cells were in lamina III itself and three were found at the border of laminae III and IV. The distribution of the different cell types encountered in laminae III and III/IV and the number of each cell class identified as being efferent to the Clare-Bishop area is shown in Table 1.

Units activated antidromically from CB were encountered only rarely (7% of all units in laminae III and III/IV). However, one particular cell type, the B cell, makes a major contribution to this number. If grouped with B_H cells (i.e. cells with the same basic response pattern as B but also showing end-zone inhibition) then 21% of the family as a whole projected to the Clare-Bishop region. No other type

TABLE 1

Distribution of different cell types in laminae III and III/IV

	S	S_H	C	C_H	B	B_H	Misc.	Unclassed
Total number in laminae III and III/IV	47	19	5	2	30	9	4	38
Number driven antidromically from CB	1	1	0	0	5	3	1	0

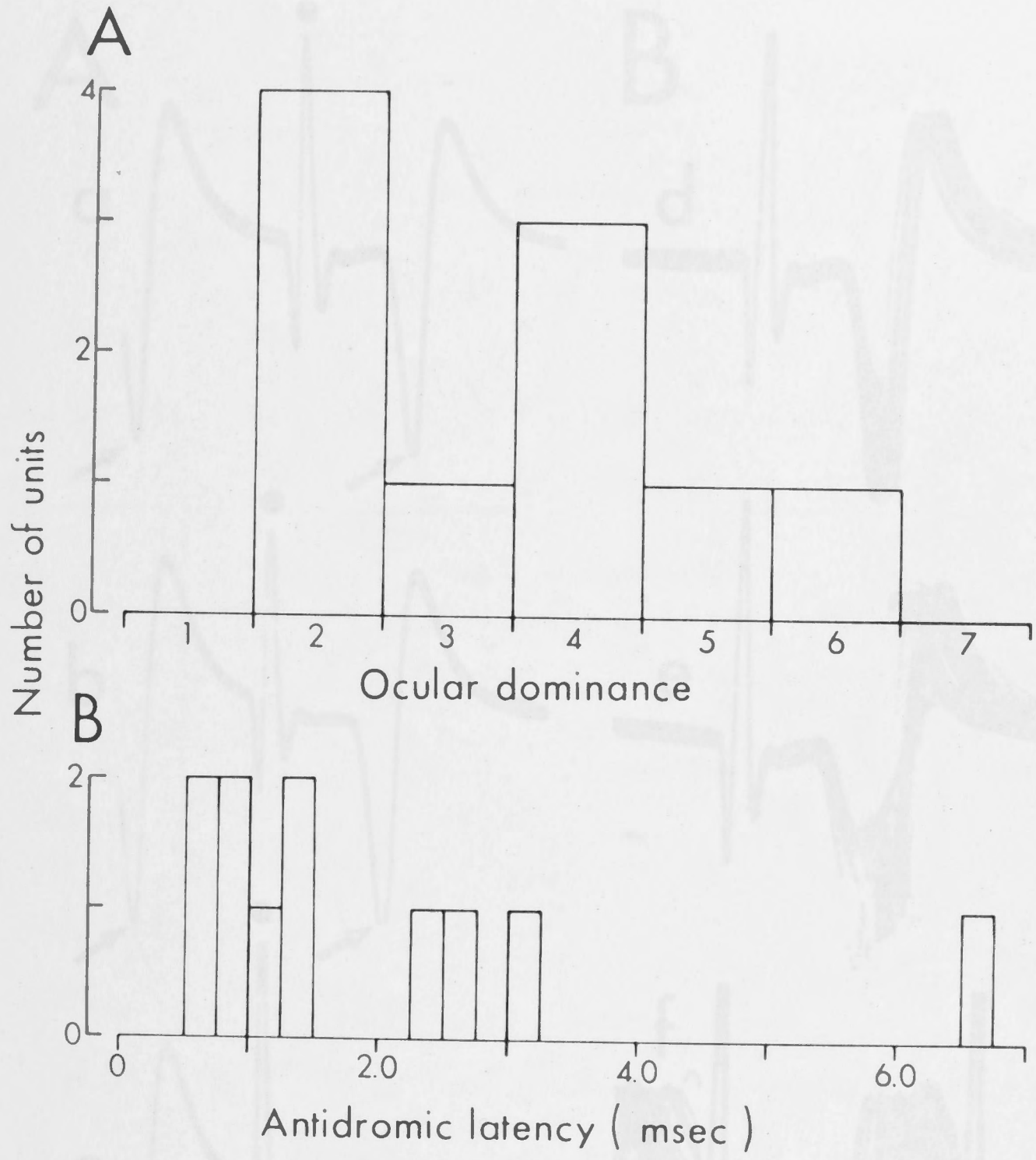


Fig. 1. A: ocular dominance distribution of striate neurons efferent to the Clare-Bishop (CB) cortex. The ocular dominance of one efferent cell was not determined. B: antidromic latencies of striate neurons projecting to CB.

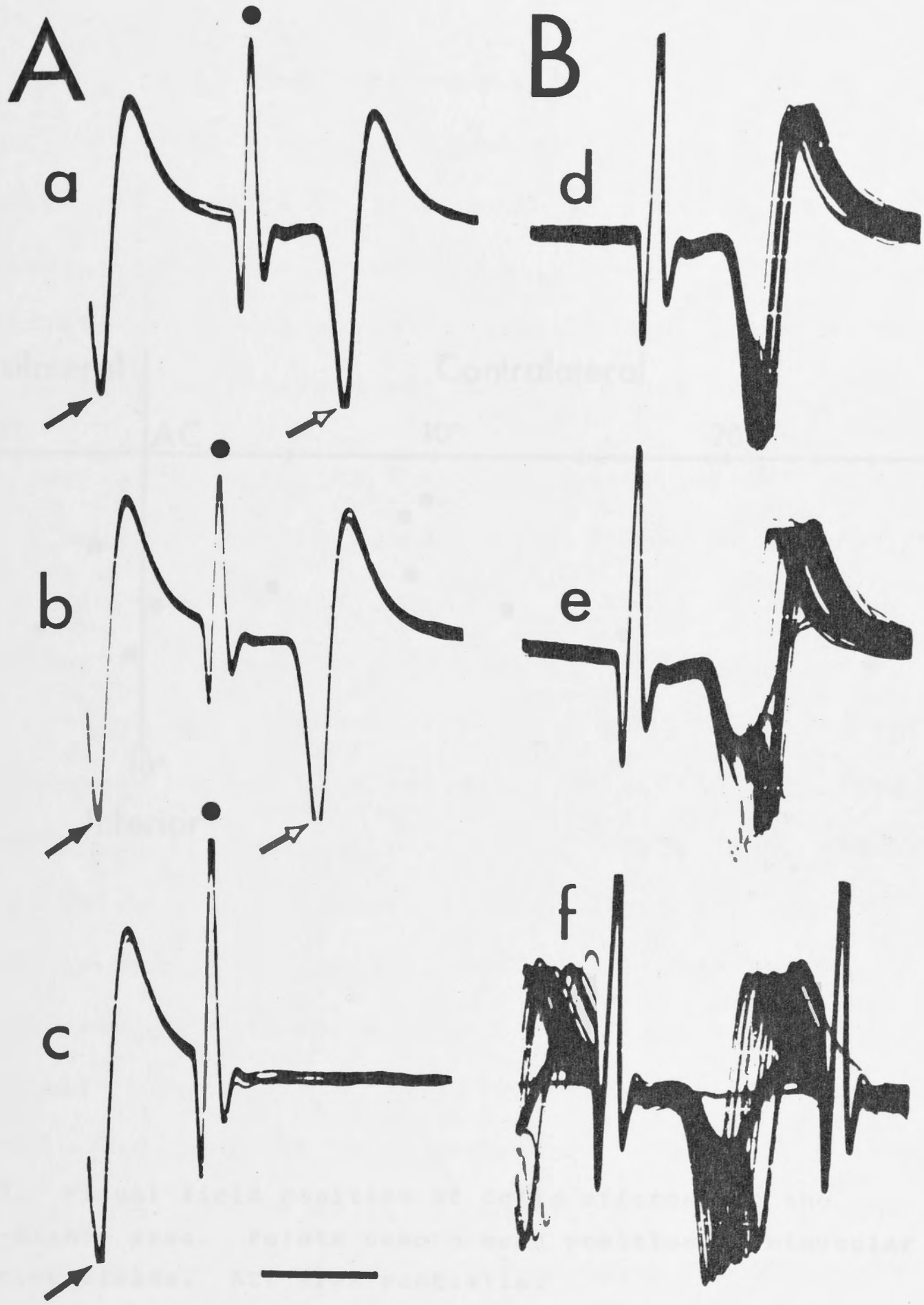


Fig. 2. Antidromic activation of a B_H cell in lamina III of area 17. A: collision of antidromic spike with an orthodromic spike elicited prior to the electrical stimulation. Filled arrow, orthodromic spike; open arrow, antidromic spike; filled circle, stimulus artifact. B: fixed latency of response and fractionation of antidromic waveform at high rates of stimulation; d, 100 Hz; e, 250 Hz; f, 500 Hz. Marker indicates 1 msec.

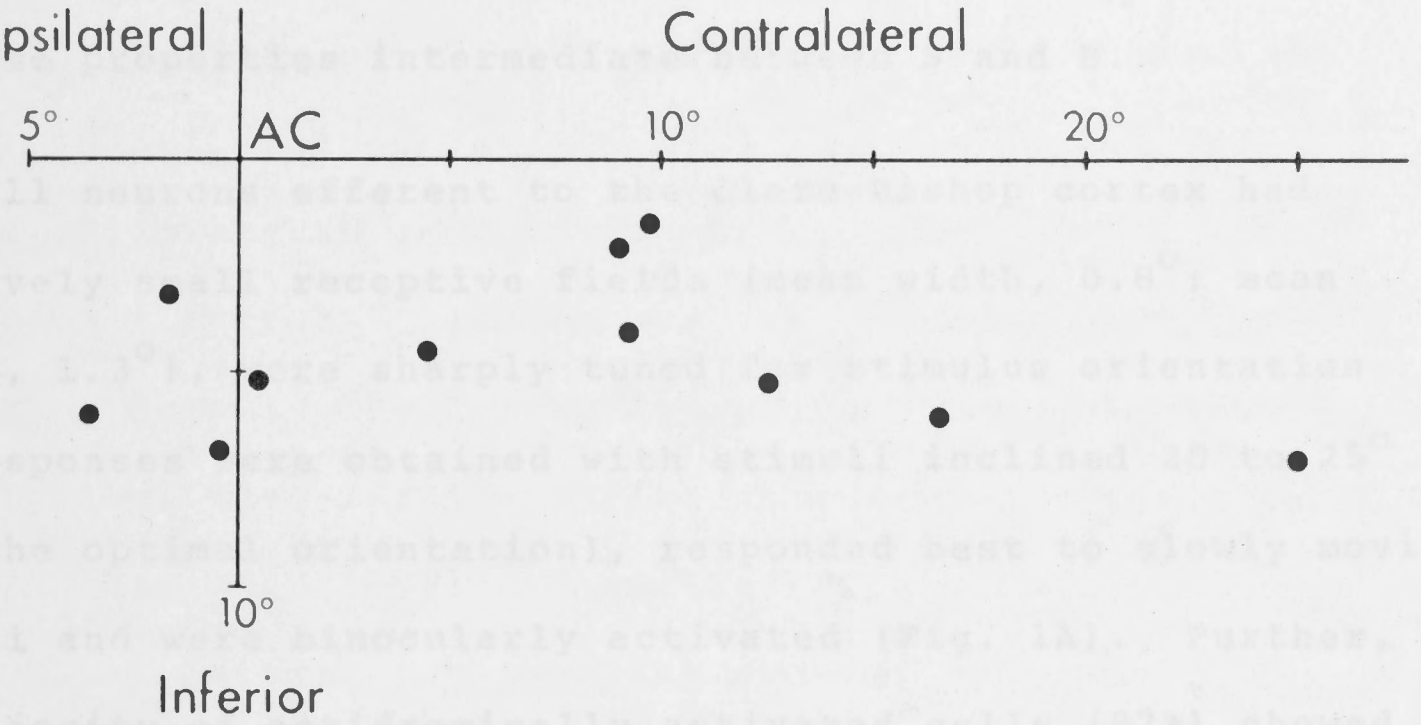


Fig. 3. Visual field position of cells efferent to the Clare-Bishop area. Points denote mean position of binocular receptive fields. AC; area centralis.

of cell had anything like this proportion of antidromic responses. The cell group described as 'miscellaneous' consisted of visually responsive cells which could not be satisfactorily placed into any of the three major receptive field families. The one antidromic unit in this class had response properties intermediate between S and B.

All neurons efferent to the Clare-Bishop cortex had relatively small receptive fields (mean width, 0.8°; mean length, 1.3°), were sharply tuned for stimulus orientation (no responses were obtained with stimuli inclined 20 to 25° from the optimal orientation), responded best to slowly moving stimuli and were binocularly activated (Fig. 1A). Further, the majority of antidromically activated cells (82%) showed a clear preference for movement in one direction. The antidromic latencies ranged from 0.6 to 6.5 msec and had a mean of 1.9 msec. An example of a lamina III, B_H cell antidromically excited from the Clare-Bishop cortex is presented in Fig. 2. The distribution of latencies is shown in Fig. 1B. None of the cells antidromically excited from the Clare-Bishop area were activated antidromically from the electrodes placed in the optic radiation. This observation taken with the fact that all of the cells projecting to the Clare-Bishop area were found to be above lamina IV, indicates that the stimulation in the lateral suprasylvian cortex was specific to that area and was not activating fibres in the underlying white matter.

Figure 3 shows the visual field position of the receptive fields of the 11 antidromically activated cells. Only one cell

had its receptive field within 4^{o} of the area centralis. Since the superficial part of most of the lateral suprasylvian gyrus appears to represent the periphery of the visual field, while the cortex deep in the medial bank of the suprasylvian sulcus contains a representation of the vertical midline (Hubel and Wiesel, 1969; Heath and Jones, 1970; Spear and Baumann, 1975a), the prevalance of peripherally located efferent cells in the present sample suggests that the stimulating electrodes were commonly situated superficially rather than deep in the Clare-Bishop area. Histological examination of the position of the stimulating electrodes confirmed that the electrodes rarely reached down to the bottom of the lateral suprasylvian area (see METHODS).

Cells orthodromically driven from the Clare-Bishop area

Fifty-two cells recorded in area 17 were orthodromically excited after electrical stimulation of the lateral suprasylvian cortex. Latencies ranged from 1.0 to 12.0 msec. Twenty-six of these cells were also orthodromically activated from the OR electrodes and in 14 cells the OR and CB latencies were very similar, which might suggest that the Clare-Bishop stimulation was not specific to that area. However, it has already been mentioned that efferent cells in area 17 were either stimulated from CB or OR but never from both. In addition afferent fibres from the dorsal lateral geniculate nucleus, as well as a substantial number of striate cortical cells, were driven from OR but not from the lateral suprasylvian cortex. These considerations indicate that much of the orthodromic CB activation was specific to that area and was not due to the

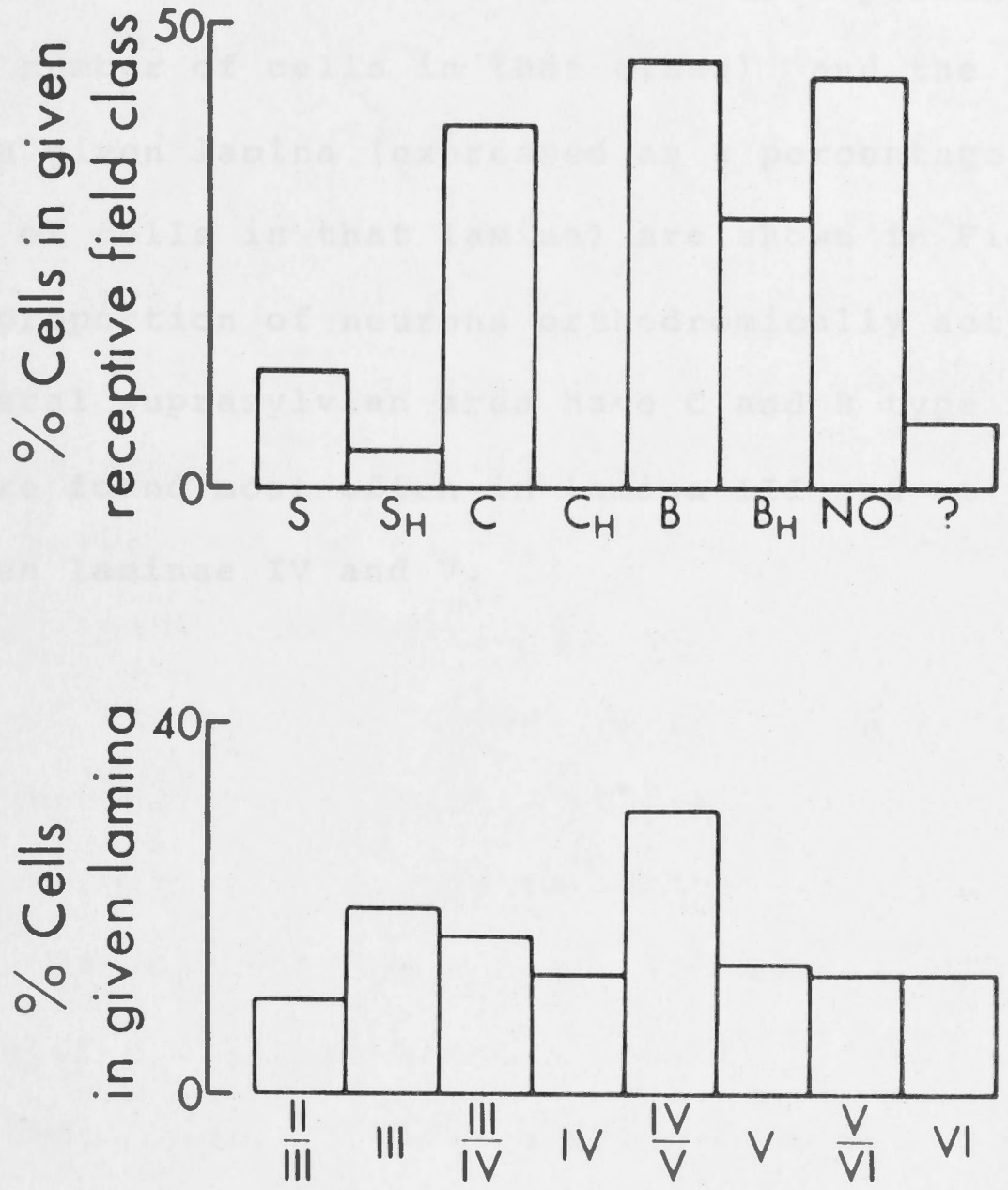


Fig. 4. The proportions of each cell class and the proportion of cells in each cortical lamina orthodromically excited by Clare-Bishop stimulation.

indirect excitation of the underlying white matter. The proportions of each cell class (expressed as a percentage of the total number of cells in that class) and the proportion of cells in a given lamina (expressed as a percentage of the total number of cells in that lamina) are shown in Fig. 4. The highest proportion of neurons orthodromically activated from the lateral suprasylvian area have C and B type receptive fields and are found most often in lamina III and at the border between laminae IV and V.

DISCUSSION

The present study has indicated that the level of processing of visual information attained in the striate cortex prior to transfer to the Clare-Bishop area is reflected, for the most part, in the receptive field properties of B cells of lamina III. It is perhaps significant that a number of cells in the B family appear to receive an input from the lateral suprasylvian cortex. Golgi studies (Cajal, 1911; O'Leary, 1941; Lorente de Nó, 1949) have indicated that small pyramidal cells in lamina VA of the striate cortex (roughly equivalent to the IV/V border zone described in this study) have recurrent axons that ascend to aborise profusely in laminae II and III. This suggests that the activity of B cells in lamina III is related to the firing of B cells situated at the IV/V border. The observation that B cells in lamina III and the IV/V border are often orthodromically driven from the Clare-Bishop cortex, while B cells in lamina III are efferent to this area, suggests a degree of reciprocity in the area 17 - CB connections which is mediated primarily by the B cell family.

Striate cells projecting to the Clare-Bishop area have small receptive fields, despite the fact that all but one of these cells were situated in cortex representing more peripheral parts of the visual field. Efferent cells are also sharply tuned for stimulus orientation, are binocularly discharged, respond best to slowly moving targets and are nearly always highly selective for the direction of movement of an optimally oriented stimulus. In comparison, cells in the lateral

suprasylvian cortex have relatively large receptive fields (though they do tend to decrease in size near the area centralis), the majority are binocularly activated and direction selective and they generally prefer faster stimulus velocities (Hubel and Wiesel, 1969; Wright, 1969; Spear and Baumann, 1975a; Camarda and Rizzolatti, 1976b). There is some disagreement as to whether Clare-Bishop neurons are orientation selective. Hubel and Wiesel (1969) have claimed that they are, whereas Spear and Baumann (1975a) suggest that this is generally not the case since the degree of direction selectivity of Clare-Bishop cells is relatively independent of the shape or orientation of a stimulus and the addition of stimulus orientation does not alter the response specificity of the cells. Finally many Clare-Bishop neurons possess inhibitory regions surrounding the excitatory discharge area (Spear and Baumann, 1975a; Camarda and Rizzolatti, 1976b).

Clearly then there are a number of important differences in the receptive field properties of striate B cells and Clare-Bishop neurons. A preliminary report (Spear and Baumann, 1975b) has described the effects of removal of areas 17, 18 and 19 on the response properties of cells in the cat lateral suprasylvian cortex. After a unilateral lesion, cells in the ipsilateral Clare-Bishop area become less direction selective and less binocular. However, a variety of receptive field properties remain unaltered; for example the responses of cells to different stimulus sizes is unaffected as is the incidence of surround inhibition. Furthermore, there is no change in the velocity sensitivity of Clare-Bishop neurons.

This result is especially surprising given that area 17 cells projecting to the lateral suprasylvian area only respond to slowly moving stimuli. The study of Spear and Baumann (1975b) therefore suggests that binocularity and direction selectivity may be dependent on the influence of corticocortical connections whereas other receptive field properties are derived from the thalamic input. However, there are clear similarities in the receptive field properties of Clare-Bishop neurons and cells in the tectothalamic system which provide much of the input to this cortical area. For example, many cells in the lateral nuclear-pulvinar complex which presumably project to the Clare-Bishop cortex (see INTRODUCTION) have large receptive fields and are direction selective (e.g. Mason, 1978). The direction selectivity of cells in the lateral suprasylvian area could thus be derived from their thalamic as well as their cortical input.

Behaviourally, the lateral suprasylvian cortex appears to be involved in visual tasks which are very similar to those mediated by the superior colliculus (Baumann and Spear, 1977; Sprague, Levy, DiBerardino and Berlucchi, 1977). Sprague *et al.*, (1977) have shown that lesions in areas 19, 21 and the lateral suprasylvian area on the one hand and lesions in the pretectum and superior colliculus on the other, result in comparable deficits in form discrimination. They suggest that the midbrain-pulvinar-cortical pathways in the cat provide the first stage in simple, coarse form perception and discrimination. Further, Kennedy and Magnin (1977) have shown that Clare-Bishop neurons are influenced by saccadic eye movements and suggest the region

is involved in oculomotor visual integration, a role also ascribed to the superior colliculus. Given the apparent uniformity of function within the tecto-pulvinar-lateral suprasylvian system, the observation that dissimilar striate receptive field types project to these areas (C cells to the tectum and pulvinar complex - Chapter 3, B cells to the Clare-Bishop area) indicates that area 17 is influencing these regions in different ways. An understanding as to why this distinction occurs will undoubtedly aid in determining the nature of the subcortical and corticocortical pathways.

CHAPTER FIVE

INTERHEMISPHERIC VISUAL CONNECTIONS

INTRODUCTION

In all vertebrates, the telencephalon is subdivided into two hemispheres which are connected by a massive commissural system. The fibres linking the two occipital lobes of the cerebral hemispheres are found in the splenium of the corpus callosum (e.g. Sunderland, 1940) and the origin and destination of these fibres has been the subject of much anatomical investigation.

In the cat, the majority of degeneration studies have shown that the termination of visual commissural fibres is restricted to the lateral part of area 17, the medial half of area 18, the lateral part of area 19 and the cortex of the suprasylvian gyrus (Hubel and Wiesel, 1967; Jones and Powell, 1968; Heath and Jones, 1970, 1972). Wilson (1968) has also described scant degeneration in the medial wall of the lateral gyrus after lesions within contralateral area 17. In most regions which receive commissural afferents,degenerating callosal terminals are found primarily in the deeper parts of lamina III and in lamina IV, and less frequently in all of the remaining cortical layers (Garey *et al.*, 1968; Jacobson and Marcus, 1970; Shoumura, 1974). However, recent reports (Fiskin, Garey and Powell, 1975; Shatz, 1977b) have indicated that the laminar distribution of callosal terminals may differ in areas 17 and 18. Fiskin *et al.*, (1975) describe dense degeneration deep in lamina III and in the upper part of lamina IV in area 18, whereas in area 17, callosal terminals are restricted to laminae III, V and VI. Shatz (1977b),

using autoradiographic methods has obtained similar results, and has also described a projection to deep layer I at the 17/18 border. All callosal fibres have asymmetric terminals and most are found on dendritic spines (Fiskin *et al.*, 1975).

Different cortical areas appear to give rise to different patterns of callosal projection. Thus after lesions at the 17/18 border, degeneration in the contralateral hemisphere is found at the 17/18 border, the lateral part of area 19 and the cortex of the suprasylvian gyrus (Hubel and Wiesel, 1967; Wilson, 1968). Lesions in area 19, however, only give rise to degeneration in the lateral part of the opposite area 19 and to the deepest part of the contralateral suprasylvian area (Heath and Jones, 1970). These authors have also shown that the lateral suprasylvian area projects only to its contralateral counterpart, the whole area being innervated by commissural fibres.

More recently, the cells of origin of callosal axons in various animals have been studied using the technique of retrograde transport of horseradish peroxidase (HRP) (Wong-Riley, 1974; Jacobson and Trojanowski, 1974; Winfield, Gatter and Powell, 1975; Innocenti and Fiore, 1976; Shatz, 1977b). In the cat, after injection of HRP at the 17/18 border, labelled cells in the contralateral cortex are found in areas 17 and 18, close to the 17/18 border (Innocenti and Fiore, 1975; Shatz, 1977b). Cells filled with HRP are found predominantly at the base of lamina III and the upper part of lamina IV although occasional cells are found in laminae II, V, VI, and the upper part of lamina III (Innocenti and

Fiore, 1976; Shatz, 1977b). Both pyramidal and stellate cells are labelled (Innocenti and Fiore, 1976). Shatz (1977b) has also described labelled cells near the lateral border of area 19 and scattered throughout the deeper layers of the Clare-Bishop cortex. This result appears to be contradictory to the study of Heath and Jones (1970) who found no degeneration in the contralateral 17/18 region after lesions confined to area 19 or the suprasylvian cortex.

Physiological mapping of the visual field in cats has shown that both the 17/18 border and the lateral part of area 19 represent the vertical midline, (Talbot, 1942; Hubel and Wiesel, 1965; Bilge, Bingle,Seneviratne and Whitteridge, 1967; Leicester, 1968; Tusa, Palmer and Rosenquist, 1978). Thus it appears that the visual callosal projection may be specifically involved in the transmission of information related to this vertical meridian. A number of studies have supported this proposal. Firstly, the receptive fields of callosal fibres recorded in the splenium have all been found to be located near the vertical midline (Hubel and Wiesel, 1967; Berlucchi, Gazzaniga and Rizzolatti, 1967; Shatz, 1977). Secondly, in cats with unilateral optic tract section (Choudhury, Whitteridge and Wilson, 1965; Vesbaesya, Whitteridge and Wilson, 1967) some visually driven units could be recorded in the cortex ipsilateral to the lesion. Visually activated cells were found only at the 17/18 border and responded to light stimuli presented near the vertical midline. Responses were abolished by cooling the corresponding points in the contralateral hemisphere and by cutting the corpus callosum.

Lastly, Shatz (1977a,b) has shown that in siamese cats, callosal projections still arise from and terminate in cortical areas which represent the vertical midline even though these regions are no longer located at the 17/18 border.

Both areas 17 and 18 receive a direct input from the ipsilateral dorsal lateral geniculate nucleus (dLGN), (Garey and Powell, 1967, 1971; Wilson and Cragg, 1967; Niimi and Sprague, 1970; Stone and Dreher, 1973; Rosenquist, Edwards and Palmer, 1974; Singer, Tretter and Cynader, 1975; Tretter, Cynader and Singer, 1975; LeVay and Gilbert, 1976; Hollander and Vanegas, 1977; LeVay and Ferster, 1977). Various physiological experiments have examined the integration of this primary pathway with the callosal projection. For example after chiasmal section, thus allowing only fibres from the ipsilateral eye to reach the dLGN, binocular cortical units were found at the 17/18 border; the response properties of the two monocular receptive fields for each cell were identical (Berlucchi and Rizzolatti, 1968). The receptive field of the ipsilateral eye is likely to be mediated by thalamocortical pathways, and the contralateral input through corticocortical connections. The convergence of primary and callosal pathways onto single cells in areas 17 and 18 has also been investigated using electrical stimulation techniques. (Toyama, Matsunami, Ohno and Tokashiki, 1974; Singer *et al.*, 1975; Tretter *et al.*, 1975; Toyama and Matsunami, 1976). The intracellular work of Toyama *et al.*, (1974) has indicated that EPSPs are evoked monosynaptically and IPSPs disynaptically in cells orthodromically activated by commissural stimulation. The observation that the primary

and commissural inputs to cortical cells might have similar organizational properties has been confirmed by Toyama and Matsunami (1976) who have shown that specific visual and callosal pathways share an inhibitory interneuron in the final common pathway to visual cells in cat cortex. Singer *et al.*, (1975) and Tretter *et al.*, (1975) have reported that cells in areas 17 and 18, with a high degree of excitatory convergence from the primary visual pathway, tend to receive the highest proportion of callosal afferents.

Although providing useful electrophysiological information on how primary and callosal pathways interact with each other, the studies just described leave unanswered a number of important questions concerning the nature of visual interhemispheric connections. For example, what are the receptive field properties of cells which send or receive commisural fibres? Do both afferent and efferent callosal cells have receptive fields close to the vertical midline of the visual field? Do cells which project through the splenium have monocular receptive fields and are cells which receive callosal fibres necessarily binocular? Lastly, is there any tendency for efferent callosal cells to prefer a particular stimulus orientation or direction of movement with respect to the midline?

In the present study an answer will be sought to the questions posed above. Single units have been recorded in areas 17 and 18, and information about their afferent and efferent commissural connectivity has been obtained by electrical stimulation of the corpus callosum (CC) and the

contralateral visual cortex (CV). As well as analysing the visual properties of cells which send or receive callosal fibres, the laminar organization and position with respect to the 17/18 border of afferent and efferent callosal cells has been compared with the anatomical distribution derived from previous neurohistological studies. Fibres were also recorded in the splenium in order to compare this overall population with the cells in areas 17 and 18 which project to the callosum. The possible role of the corpus callosum in vision is discussed in light of these results.

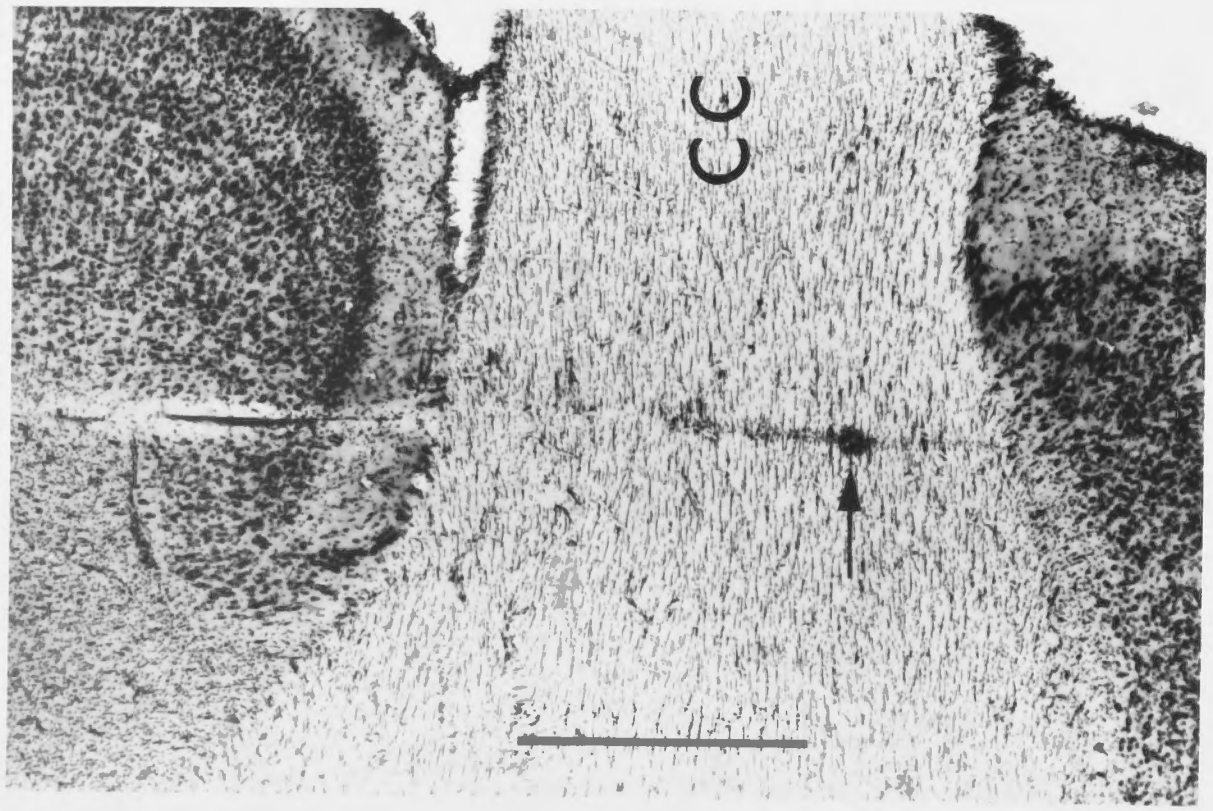
METHODS

The general methods employed in these experiments have already been described (Chapter 1). All experiments were performed on anaesthetized (N_2O/O_2), paralysed (toxiferine and gallamine triethiodide) cats. Pupils were dilated with atropine and the cornea protected with contact lenses. Artificial pupils (3 mm diameter) were used and the animals refracted for a viewing distance of one metre. Retinal landmarks were back-projected onto a tangent screen using an indirect opthalmoscope (Zeiss Fundus Camera).

Two types of experiment have been undertaken. In the first, tungsten in glass microelectrodes (Levick, 1972) were used to record from single fibres in the splenium of the corpus callosum. Histological checks were generally carried out on successful penetrations to confirm that the electrode had passed through the splenium. In addition, electrolytic lesions were usually made during, or at the end of, recording tracks to confirm the site of recording of the callosal axons. Such a penetration is shown in Fig. 1.

In the second part of the study, tungsten in glass micro-electrodes were used to record extra-cellularly from single units in areas 17 and 18 of the visual cortex. All penetrations were made between Horsley-Clark Posterior 1 and 5 and were angled to pass tangentially across the border between areas 17 and 18 within the lateral bank of the lateral gyrus. As in all experiments, electrolytic lesions were made at various intervals along the penetration of the

Fig. 1. Photomicrograph of an electrode penetration through the splenium of the corpus callosum (CC). An electrolytic lesion is shown by the arrow. Marker indicates 1 mm.



recording electrode. After sacrifice of the animal, 40μ Nissl-stained sections were prepared and the electrode tracks reconstructed. To investigate the afferent and efferent connectivity of these units, platinium/iridium glass-insulated stimulating electrodes were placed in the corpus callosum (CC), the contralateral visual hemisphere (CV) and occasionally in the optic chiasm (OX) and ipsilateral optic radiation (OR).

For callosal stimulation a linear array of 4 electrodes, each 2 mm apart was stereotaxically positioned between Horsley-Clark anterior 2 and anterior 8, about 1.5 mm lateral to the midline, contralateral to the recording hemisphere. From the experiments which involved recording from the splenium of the CC itself, it was known at what depths visual fibres could be found. This was used as a guide to the depth of the callosal stimulating electrodes. In some cats, the threshold of activation of cells driven from the corpus callosum was measured while the depth of the callosal electrodes was varied. The depth at which the lowest threshold (for 100% response) was obtained was then used in these experiments. The posterior pair of electrodes always had the lowest thresholds, and the most anterior pair the highest. This correlates well with the fact that visual commissural fibres pass through the posterior third of the callosum.

The number of CV stimulating electrodes varied from 6 to 9. A diagrammatic representation of their position with respect to the recording electrode is shown in Fig. 2. The electrodes

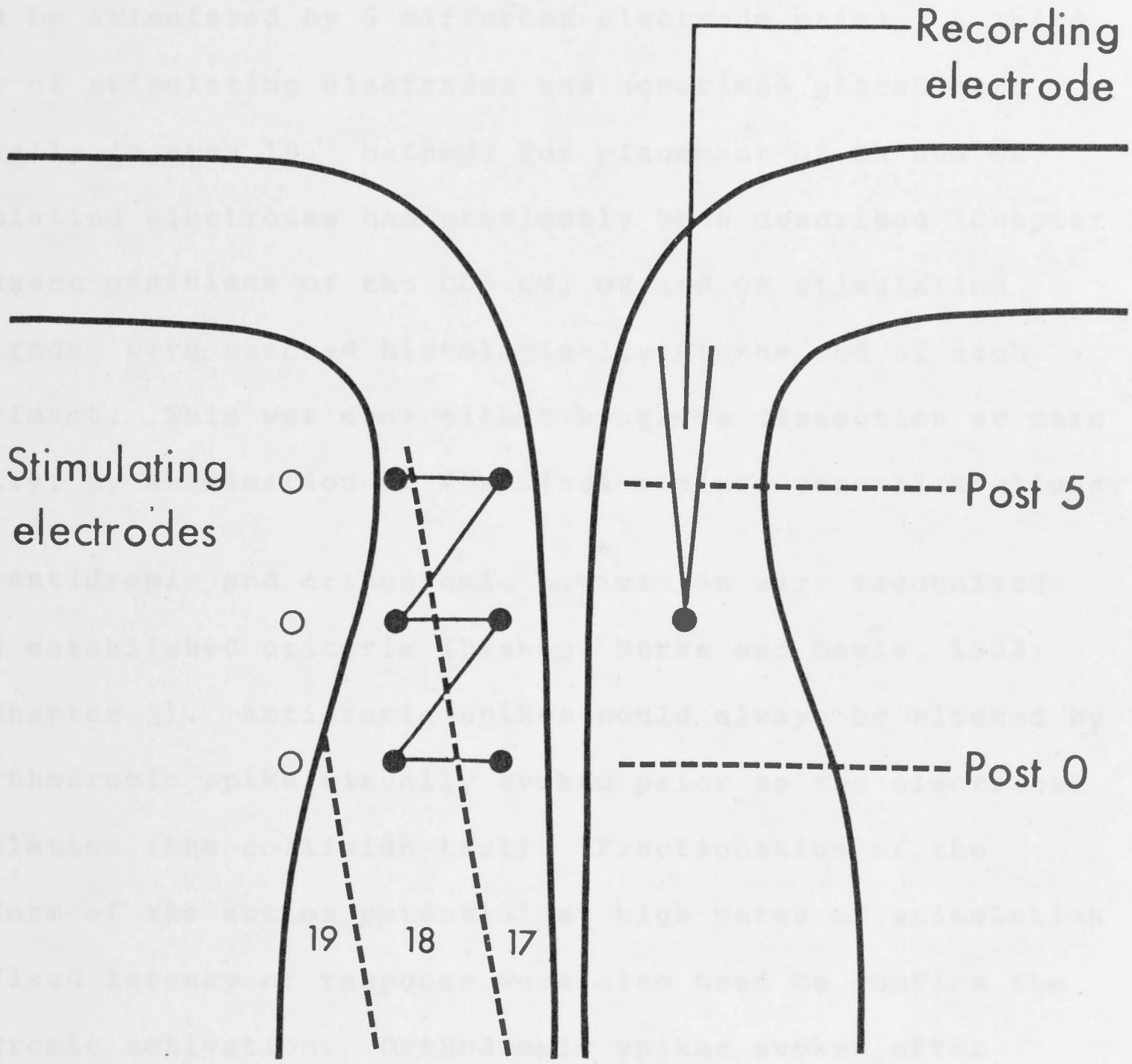


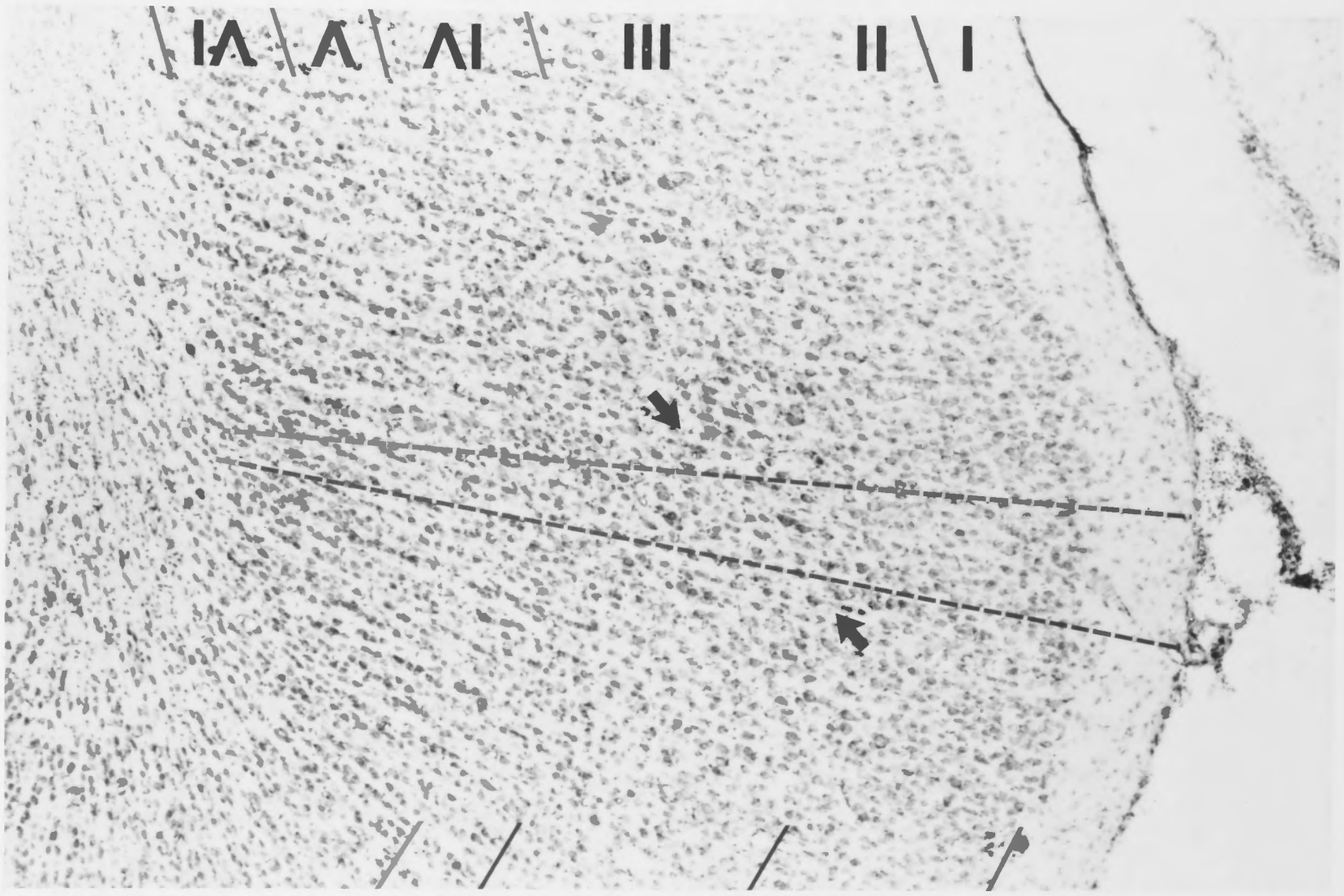
Fig. 2. Representation of the location of the recording electrode and CV stimulating electrodes. For the stimulating electrodes: filled circles, electrodes always used; open circles, electrodes sometimes used. Lines joining filled circles indicate possible bipolar stimulating combinations.

were arranged to be in a corresponding position to the site of recording in the contralateral hemisphere. The 17/18 border could be stimulated by 5 different electrode pairs. A third array of stimulating electrodes was sometimes placed more laterally in area 19. Methods for placement of OX and OR stimulating electrodes has previously been described (Chapter 1). The exact positions of the CC, CV, OX and OR stimulating electrodes were checked histologically at the end of each experiment. This was done either by gross dissection or more usually, by examination of 40μ Nissl-stained coronal sections.

Antidromic and orthodromic activation were recognized using established criteria (Bishop, Burke and Davis, 1962; cf. Chapter 3). Antidromic spikes could always be blocked by an orthodromic spike visually evoked prior to the electrical stimulation (the collision test). Fractionation of the waveform of the action potential at high rates of stimulation and fixed latency of response were also used to confirm the antidromic activation. Orthodromic spikes evoked after electrical stimulation could not be collided with a visually produced spike, they did not have a fixed latency of response and they invariably failed to follow high rates of stimulation.

The laminar pattern of areas 17 and 18, and the location of the border between these two areas was identified in Nissl-stained preparations using established criteria (O'Leary, 1941; Otsuka and Hassler, 1962; Garey, 1971). For this study, lamina IV of area 18 was not subdivided into two parts (Chapter 2). The cytoarchitectonic criteria used to define the 17/18 border in the present study are outlined below:

Fig. 3. Photomicrograph of Nissl-stained section showing 17/18 border zone. Dotted lines indicate limits of border region. Arrows show the position of large pyramidal cells located deep in lamina III.


I
II
III
IV
V
VI

(i) A number of large pyramidal cells are located in lamina III at the 17/18 border.

(ii) Layer IV becomes narrower as one progresses from area 17 to area 18. Concomitant with this, the medium to large pyramids of lamina III are found much deeper in the cortex in area 18 than in area 17.

(iii) There is a widening of lamina V in area 18, adjacent to area 17.

Previous reports have commented on the difficulty of identifying the 17/18 border in the cat and in the present work is was not possible to identify an exact point at which area 17 stopped and area 18 began. Rather, there appeared to be a zone, 150 to 250μ wide which could not be safely designated as either striate or parastriate in character. This region is termed the *17/18 border zone* and is shown in Fig. 3. The two dotted lines indicate the limits of this transition area. Area 17 is above the zone, and area 18 below it. In most of the following analysis, units located in this zone have been placed in a separate group from those definitely located in areas 17 and 18.

Receptive fields in both the splenial and cortical experiments were plotted using hand held visual stimuli, and were analysed using established criteria (Hubel and Wiesel, 1962, 1965; Bishop and Henry, 1972; Henry, 1977). S cells (both in areas 17 and 18) had separate response regions to moving light and dark edges, and separate ON and OFF areas to

stationary flashing stimuli. Some units only responsed to one edge and had just one ON or OFF stationary flashing light area. These units have generally been included in the S cell group. The exception to this rule, the A cell, is discussed below. S cells typically had low spontaneous activity and were sharply tuned for stimulus orientation. C cells in areas 17 and 18 were characterised by having superimposed dark and light edge response regions and gave mixed ON/OFF discharges when tested with stationary stimuli. They usually had a relatively high spontaneous activity and were broadly tuned for orientation. B cells have been previously described in both area 17 (Henry, Lund and Harvey, 1978; Chapter 1) and area 18 (Chapter 2). They resembled C cells in having superimposed dark and light edge fields and mixed ON/OFF responses to flashing bars, but they preferred slower velocities, had low spontaneous activity, had smaller receptive fields and were more tightly tuned for stimulus orientation. Units designated as A cells resembled S cells in that they had separate response regions to moving light and dark edges and separate stationary ON and OFF zones, but they had larger fields and their response to moving stimuli did not peak at a point but was maintained across the whole length of the receptive field (Henry, 1977). End zone inhibition was sometimes present in all of the above receptive field classes, and as suggested by Henry (1977), these cells have been designated S_H, C_H, B_H, and A_H. Some non-oriented units were also encountered whose responses to electrical stimulation of the ipsilateral OR indicated that they were postsynaptic to geniculocortical fibres (cf. Chapter 1 and 2). Some units did not respond to stationary flashing

stimuli, but it was always possible to place these cells in one of the various receptive field categories (S, C, B or A) on examination of their other response characteristic (e.g. spontaneous activity, orientation tuning, receptive field size and responses to moving edges).

RESULTS

P A R T O N E

RECORDING FROM FIBRES IN THE SPLENIUM OF THE CORPUS CALLOSUM

In this section, the visual properties of single fibres recorded in the splenium of the corpus callosum (CC) are described. In 9 cats, 60 fibres were isolated in 22 successful penetrations. Visual fields could be plotted for 31 of these fibres, a further 12 axons were driven visually but were not held long enough to allow classification, and 17 could not be activated by visual stimuli. The depths from the cortical surface at which visual callosal fibres were encountered ranged from 10.6 to 13.0 mm and there was a tendency for non-visual fibres to be located in the deeper parts of the splenium.

As would be expected from the number of visual cortical areas which send axons through the CC, a great variety of receptive field types were found in the splenium. The receptive fields of 27 fibres could be satisfactorily characterised. The classification scheme was based on that proposed by Henry (1977) (see METHODS), although this had to be extended to include receptive fields of axons which were presumably derived from cells in more lateral visual cortical areas. The receptive fields found in the CC are shown in Table 1. No receptive fields were studied which could be uniquely ascribed to area 17. The 5 fibres with S type properties (three S and two S_H) were more typical of area 18 than area 17 (see Chapter 2). The C and C_H cells could have

TABLE 1

Receptive field classes recorded in the splenium
of the corpus callosum

	S	S_H	C	C_H	B_H	A_H	Large-field	Non-oriented	Visual but not classified
No. of units	3	2	5	7	1	2	2	5	4

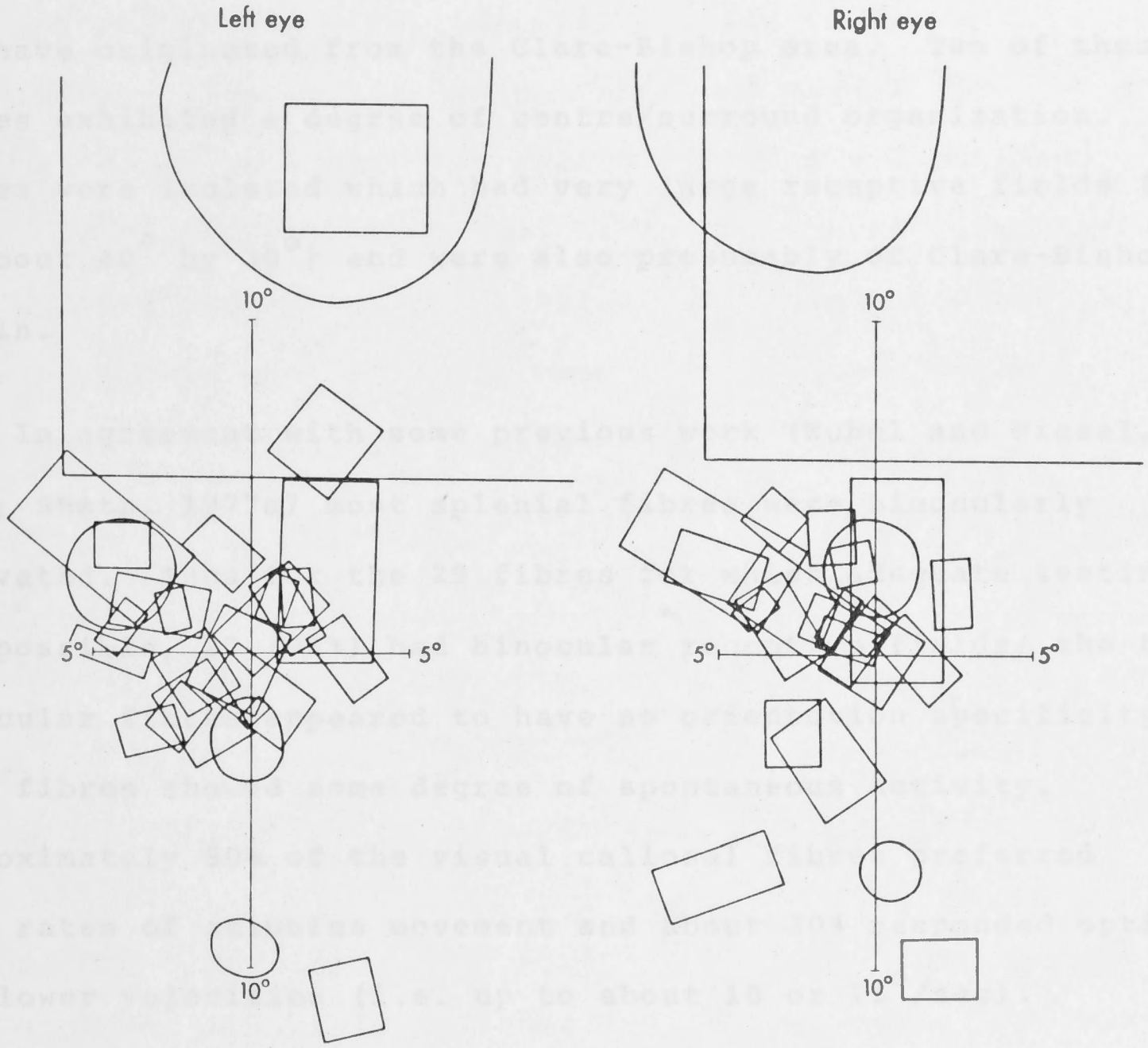


Fig. 4. Visual field position of the receptive fields of fibres recorded in the splenium of the corpus callosum. Receptive fields in each eye are shown separately and are plotted with respect to a standardized area centralis position. The area centralis is represented by the intersection of the vertical and horizontal lines.

originated from either area 17, or more likely from areas 18 or 19 since cells of this type are more common in these two areas. Five fibres had little or no orientation specificity and these may have originated from the Clare-Bishop area. Two of these fibres exhibited a degree of centre/surround organization. Two fibres were isolated which had very large receptive fields (up to about 40^{o} by 30^{o}) and were also presumably of Clare-Bishop origin.

In agreement with some previous work (Hubel and Wiesel, 1967; Shatz, 1977a) most splenial fibres were binocularly activated. Thus for the 29 fibres for which adequate testing was possible, 27 (93%) had binocular receptive fields; the two monocular fibres appeared to have no orientation specificity. Most fibres showed some degree of spontaneous activity. Approximately 50% of the visual callosal fibres preferred high rates of stimulus movement and about 30% responded optimally to slower velocities (i.e. up to about 10 or 15^{o}/sec).

The visual field location of the receptive fields of the callosal fibres are shown in Fig. 4. All receptive fields have been plotted with respect to a standardized area centralis position; left eye fields are shown in A and right eye fields in B. All units had receptive fields close to the vertical midline, in agreement with earlier reports (Hubel and Wiesel, 1967; Berlucchi *et al.*, 1967; Shatz, 1977a). It should be emphasised that the relationship between the receptive field positions and the vertical midline is only approximate since estimates of the area centralis position are subject to errors of perhaps ½ to 1^{o} in some circumstances. In addition no

correction for cyclo-rotation of the eyes has been made.

In terms of elevation in the visual field, the majority of callosal fibres had receptive fields close to the area centralis, in agreement with earlier work (Hubel and Wiesel, 1967). This is of interest in light of a recent report (Innocenti and Fiore, 1976) which showed that, after unilateral injection of HRP into the visual cortex, labelled cells in the opposite hemisphere were most numerous when the injection was made in the locus of the cortical representation of the area centralis. Thus it appears that the central visual field may give rise to a substantial part of the callosal projection.

P A R T T W O

SINGLE UNIT RECORDING IN AREA 17 AND AREA 18

Although recording from fibres in the splenium is useful in indicating the type of visual information being transmitted from one hemisphere to the other, there are important limitations to this type of experiment. Firstly, it is usually not possible to identify the exact visual cortical area from which the axons originate. Hence physiological findings cannot be correlated with the cytoarchitectonic and laminar distributions of afferent and efferent commissural pathways previously determined using anatomical techniques. Secondly, in terms of visual field position and receptive field classification, splenial recording only allows study of the cells of *origin* of the commissural system. No information can be obtained about the cells which *receive* this callosal projection.

In this second part of the study, single units have been recorded during penetrations through the lateral bank of the lateral gyrus. Information about the afferent and efferent connections of the cortical cells was obtained by electrical stimulation of the CC and CV (see METHODS and Fig. 2). In 4 cats, electrodes were placed only in the CC. The data are taken from experiments performed on 20 adult cats.

Responses to electrical stimulation of CC and CV

Electrical stimulation of the commissural system was tested on 417 of the units encountered in areas 17 and 18. Ninety-five (23%) were activated orthodromically and 15 (4%) antidromically after stimulation of CC and/or CV. The proportion of orthodromically activated units found in the present study (although largely dependent on the recording site and its relation to the 17/18 border) is similar to that described by Singer *et al.*, (1975) and Tretter *et al.*, (1975), who reported that about 30% of cells recorded in areas 17 and 18 received an input from the opposite hemisphere. Eighty-three orthodromically excited units were recorded in cats in which both CC and CV stimulating electrodes were present; 30 units could be activated *orthodromically* only from CC, 24 only from CV, and 29 could be activated from both sites. Seven *antidromic* units were activated only from CC and 4 from both CC and CV. Thresholds for CV stimulation were usually higher than for CC stimulation. Thus the absence of a response to CV stimulation in some cells driven from CC does not necessarily imply that the afferent or efferent axons were coming from, or going to, an area of contralateral cortex other than the 17/18 border region.

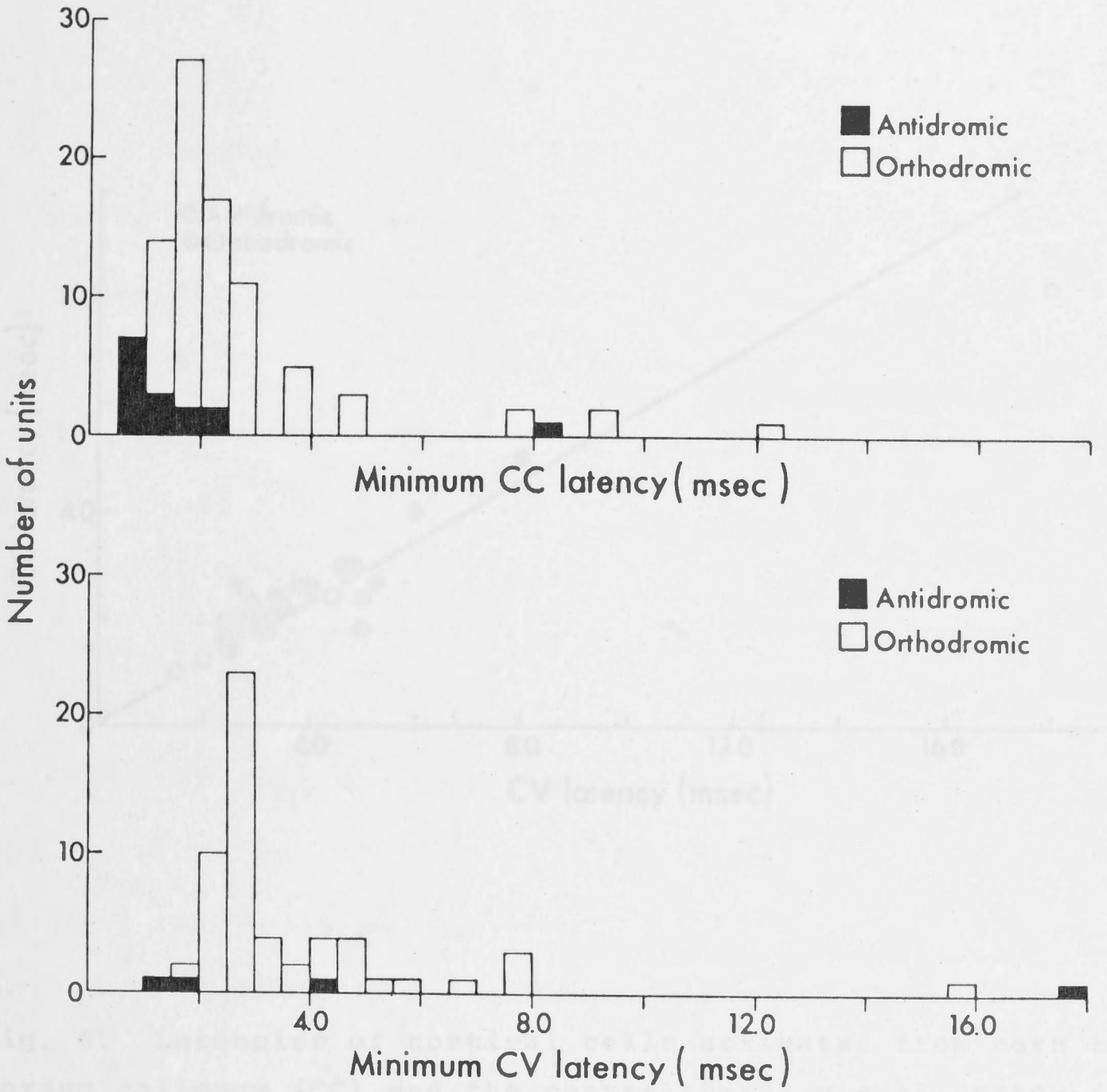


Fig. 5. Antidromic (filled blocks) and orthodromic (open blocks) latencies of cortical cells activated after electrical stimulation of the corpus callosum (CC) and contralateral visual cortex (CV).

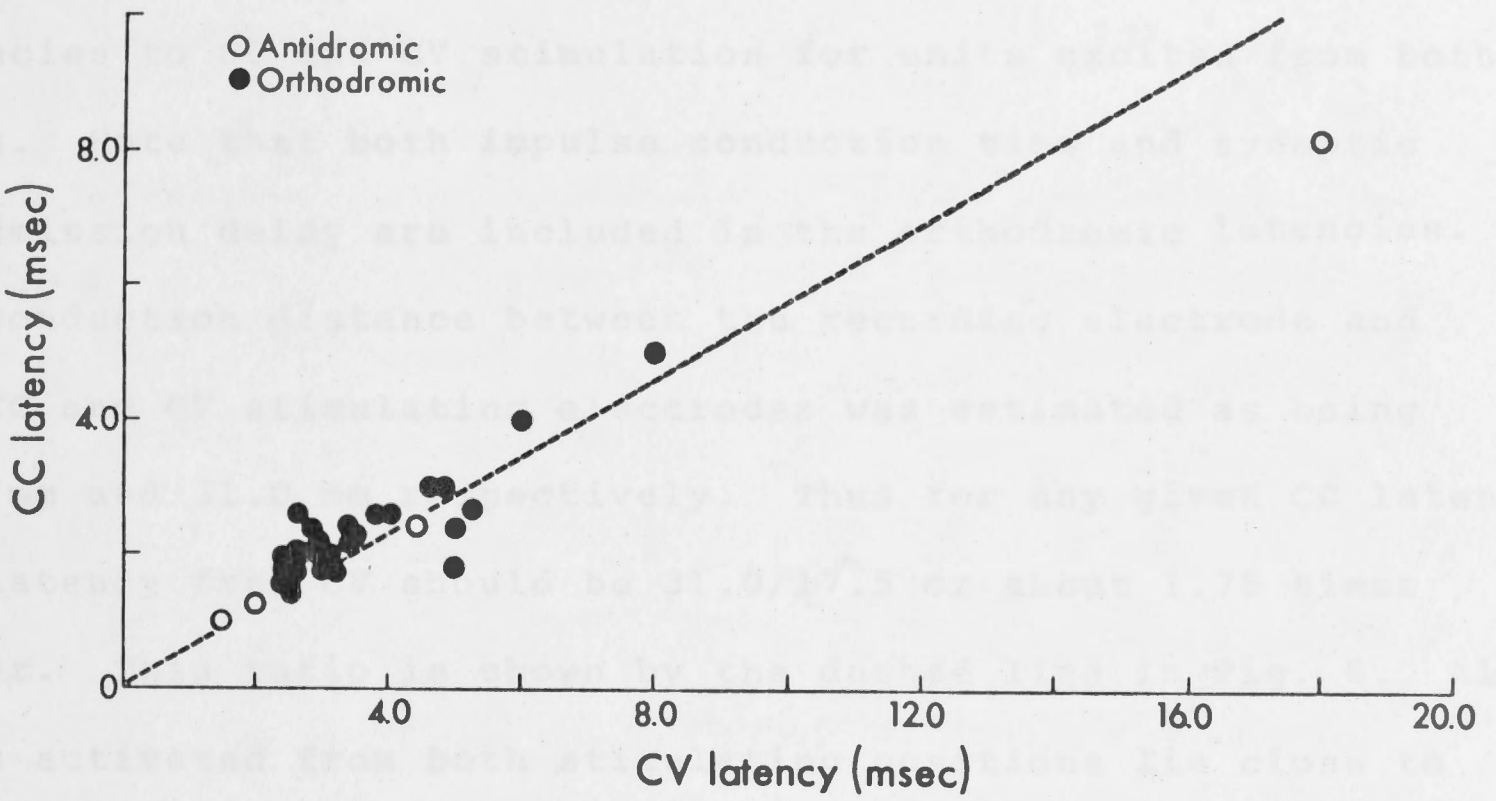


Fig. 6. Latencies of cortical cells activated from both the corpus callosum (CC) and the contralateral visual cortex (CV). Filled circles, orthodromic activation; open circles, antidromic activation. Dashed line; ratio of CV/CC conducting distances.

The latencies to CC and CV stimulation are shown in Fig. 5. In each histogram, antidromically and orthodromically activated units are shown as filled and open blocks respectively. With one exception (8.1 msec), the antidromic latencies to CC stimulation ranged from 0.8 to 2.5 msec. Figure 6 shows the latencies to CC and CV stimulation for units excited from both sites. Note that both impulse conduction time and synaptic transmission delay are included in the orthodromic latencies. The conduction distance between the recording electrode and the CC and CV stimulating electrodes was estimated as being 17.5 mm and 31.0 mm respectively. Thus for any given CC latency, the latency from CV should be 31.0/17.5 or about 1.75 times longer. This ratio is shown by the dashed line in Fig. 6. All units activated from both stimulating positions lie close to this line; thus for orthodromically activated units, differences in absolute latencies may be due to variation in the size and conduction velocity of afferent commissural fibres, rather than in the number of synapses interposed between the presynaptic fibre and the cell being stimulated. In support of this contention, Toyama *et al.*, (1974) have shown that in cat areas 17 and 18, EPSP's are evoked monosynaptically and IPSP's disynaptically after commissural stimulation. Indeed, the fit of the orthodromically excited cells is even better if one synaptic transmission delay is subtracted from the latencies presented in Fig. 6.

The relationship between callosally driven units and the 17/18 border

The laminar position and location with respect to the 17/18 border were histologically determined for 313 of the units tested

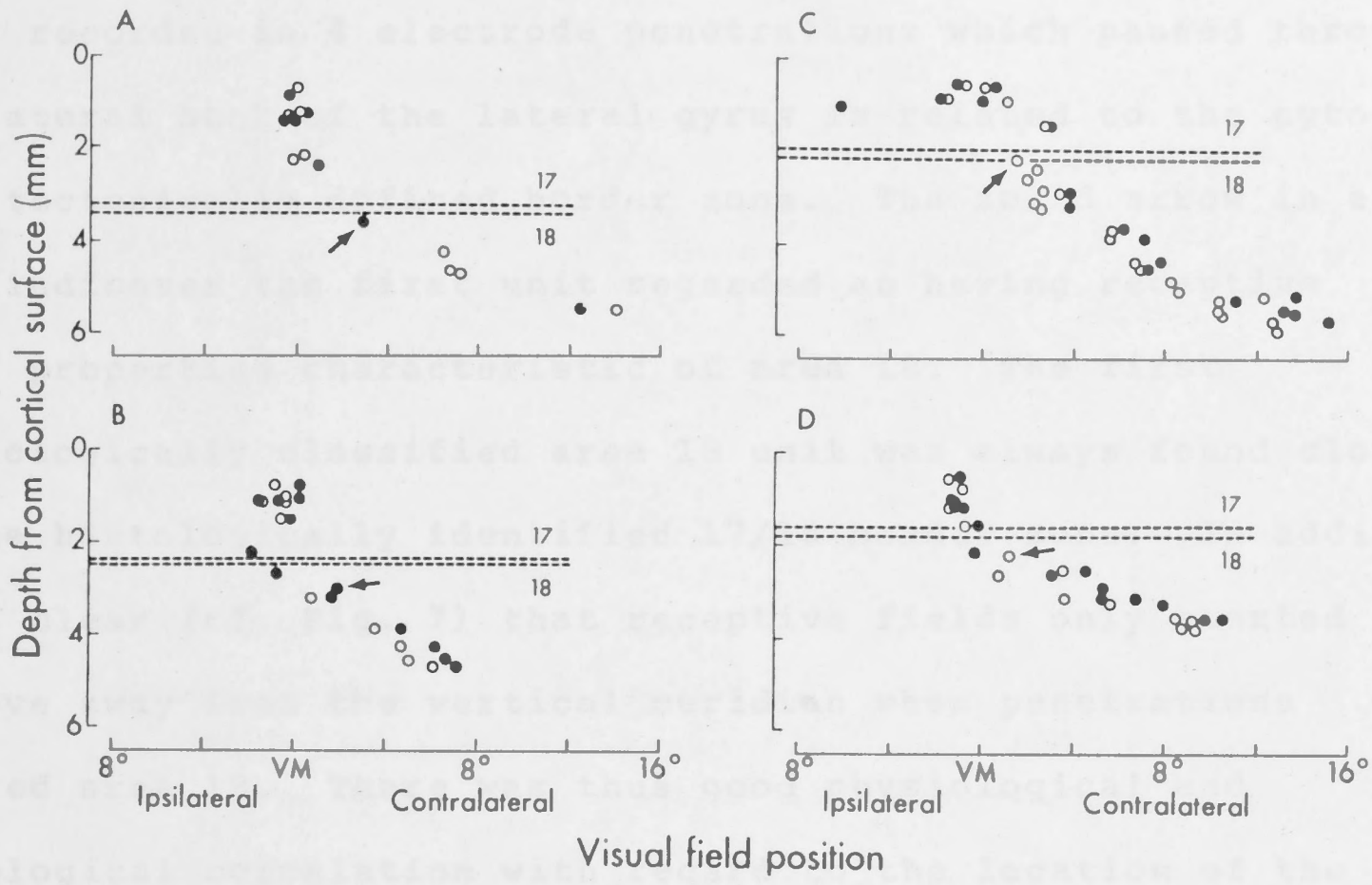


Fig. 7. A-D: visual field position of the receptive fields of cortical units plotted against depth from cortical surface. Filled circles, right (contralateral) eye; open circles, left (ipsilateral) eye. In each graph, the extent of the 17/18 border zone is shown by the two dotted lines. Arrows indicate first unit regarded as having receptive field properties characteristic of area 18.

by commissural stimulation. The difficulty of accurately locating the 17/18 border has already been mentioned (see METHODS). In Fig. 7, the visual field position of single units recorded in 4 electrode penetrations which passed through the lateral bank of the lateral gyrus is related to the cyto-architectonically defined border zone. The solid arrow in each plot indicates the first unit regarded as having receptive field properties characteristic of area 18. The first physiologically classified area 18 unit was always found close to the histologically identified 17/18 border zone. In addition, it is clear (cf. Fig. 7) that receptive fields only started to move away from the vertical meridian when penetrations entered area 18. There was thus good physiological and histological correlation with regard to the location of the border zone between striate and parastriate cortex. If there is a representation of the vertical midline in area 18, it is very small and extends no more than about 0.5 mm from the 17/18 border zone.

Of the 313 units whose histological position was determined, 107 were in area 17, 34 were located within the 17/18 border zone, and 172 were found in area 18. Sixty-nine (22%) units could be orthodromically activated and 13 (4.2%) antidromically activated after electrical stimulation of the commissural system. Table 2 shows the percentage of orthodromically and antidromically activated units in the three regions. From the percentages of antidromically activated units it appears that units within the 17/18 border zone give rise to the largest proportion of callosal axons.

TABLE 2

The proportion of orthodromically and antidromically activated units in areas 17 and 18 and the 17/18 border region

Cortical area	17	17/18	18
Total number of units	107	34	172
%Orthodromic	21.5	23.5	22.1
%Antidromic	3.7	11.8	2.9

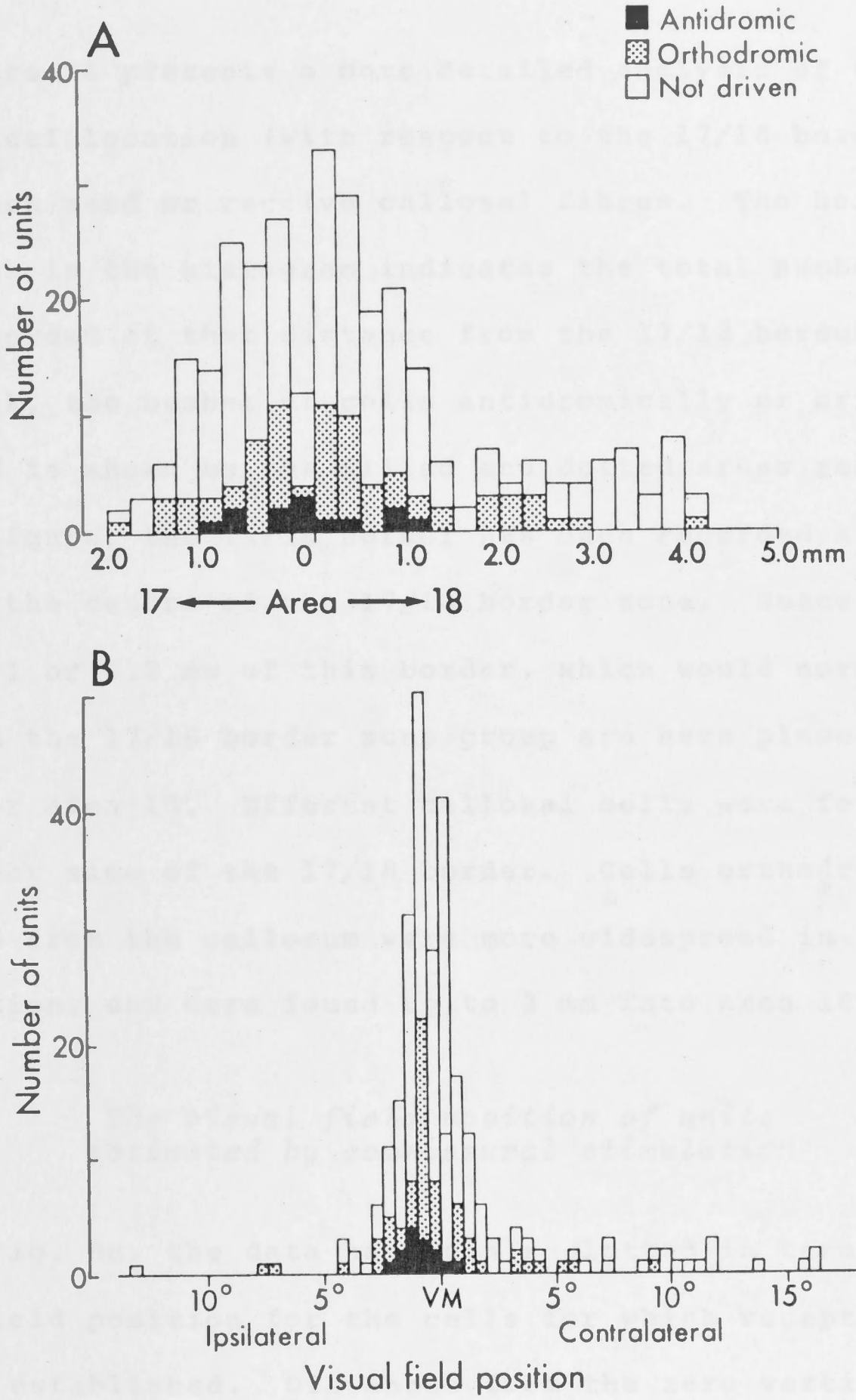


Fig. 8. Histological location and visual field position of cells tested by electrical stimulation of the corpus callosum (CC) and contralateral visual cortex (CV). A: position with respect to the 17/18 border. B: position with respect to the visual vertical midline (VM). Filled blocks, antidromically activated cells; dotted blocks, orthodromically activated cells; open blocks, cells not excited from CC or CV.

Figure 8A presents a more detailed analysis of the histological location (with respect to the 17/18 border) of cells which send or receive callosal fibres. The height of each block in the histogram indicates the total number of cells recorded at that distance from the 17/18 border. Within each block, the number of cells antidromically or orthodromically activated is shown by the filled and dotted areas respectively. In this figure, the 17/18 border has been regarded as a discrete point at the centre of the 17/18 border zone. Hence units within 0.1 or 0.2 mm of this border, which would normally be placed in the 17/18 border zone group are here placed in either area 17 or area 18. Efferent callosal cells were found within 1 mm either side of the 17/18 border. Cells orthodromically activated from the callosum were more widespread in their distribution, and were found up to 3 mm into area 18.

The visual field position of units activated by commissural stimulation

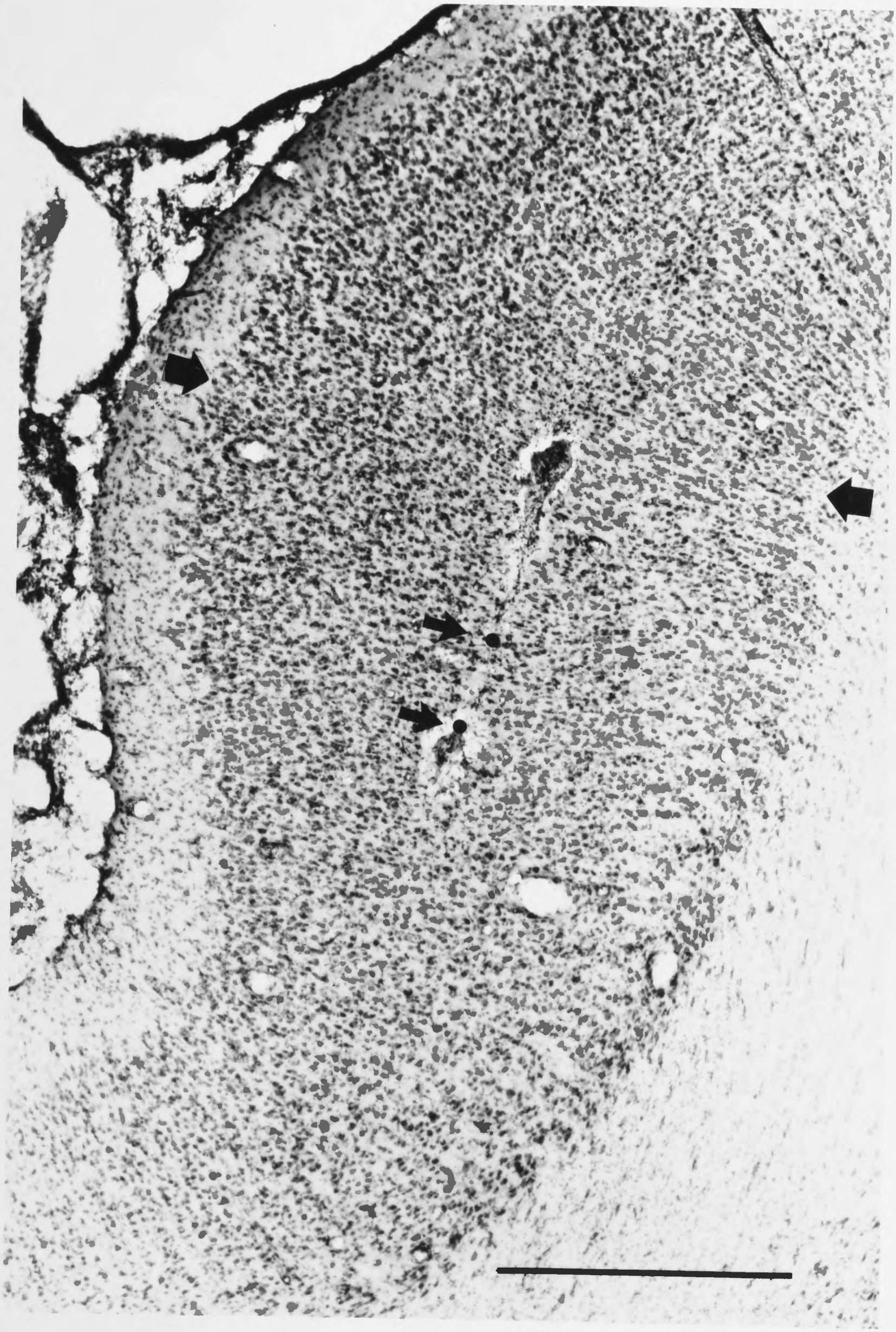
In Fig. 8B, the data has been replotted in terms of visual field position for the cells for which receptive fields could be established. Distances from the zero vertical meridian were measured from the centre of each receptive field and, for binocular units, the average receptive field eccentricity for the two eyes has been used. Efferent callosal cells had receptive field centres close to the vertical midline, however, some cells receiving afferent commissural fibres had fields up to 9^{o} into the *contralateral* and up to 8^{o} into the *ipsilateral* visual field.

From Fig. 8B, many units recorded close to the 17/18 border zone had receptive fields apparently in the *ipsilateral* visual hemifield. These units were nearly always recorded on the area 17 side of the border (cf. Fig. 7). An exact statement concerning the extent of the ipsilateral visual field representation in the visual cortex is not possible due to the errors in defining the area centralis and the orientation of the vertical midline in the paralysed cat (see earlier). However, any consistent errors that might occur, for example if the peak ganglion cell density does not coincide with the centre of the blood vessel pattern normally employed to identify the area centralis, would tend to cancel out since the data in Fig. 8B contains visual fields from both the ipsilateral and contralateral eyes. Given the possible errors (up to perhaps 2^{o}) in relating the position of a cell's visual field with the vertical midline, there were still some units with receptive fields which appeared to be in the ipsilateral visual hemifield. Although the majority of these units were found to be only 1 or 1.5^{o} into the ipsilateral visual field (cf. Nikara, Bishop and Pettigrew, 1968; Leicester, 1968; Blakemore, 1969; Tusa, Palmer and Rosenquist, 1977), some units had receptive fields much further out; the most distant unit was found about 13^{o} in the ipsilateral hemifield. Nearly all of these peripheral units were driven only by the contralateral eye.

The laminar distribution of callosally activated units

An example of an electrode track in the lateral bank of the lateral gyrus is presented in Fig. 9. Two lesions are

Fig. 9. Photomicrograph of electrode penetration in the lateral bank of the lateral gyrus. Small arrows indicate position of two cells antidromically activated from the corpus callosum. Both units are located just in area 18 near the border between laminae III and IV. Large arrows, 17/18 border region; marker, 1 mm.



clearly visible. The position of two cells antidromically activated from the callosum are indicated by the arrows. Both cells were located deep in lamina III of area 18, within a millimetre of the 17/18 border.

Table 3 shows the number of units in each lamina of area 17, the 17/18 border zone and area 18 that were orthodromically or antidromically activated by electrical stimulation of the commissural pathways. The total number of cells recorded in each layer is also shown. Two cells were activated both antidromically and orthodromically after CC stimulation. The percentage of orthodromically and antidromically activated units in each lamina, pooling data from all three areas, is shown in Fig. 10. Efferent callosal units were predominately located in lamina III, and were found most often in deep III at the III/IV border (cf. Fig. 9). Cells receiving commissural fibres were found throughout all cortical layers, the highest percentage of afferent cells occurring in laminae II, III and the IV/V border.

Receptive field properties of units activated from CC and CV

Of the 313 units located histologically, 186 were classified according to receptive field class using established criteria (see METHODS). The number of the various receptive field types in area 17, the 17/18 border region and area 18 orthodromically or antidromically activated by commissural stimulation is shown in part A of Table 4. In part B of Table 4, the percentage of afferent and efferent cells for each class is shown. In Fig. 11, the data for each receptive field type has

TABLE 3

Laminar distribution of orthodromically and antidromically activated units

		L A Y E R							
AREA		II,	III,	III/IV,	IV,	IV/V	V,	V/VI,	VI
17	Total number of units	21	27	13	20	6	7	7	6
	Orthodromic	7	6	2	2	2	2	0	2
	Antidromic	0	0	3	1	0	0	0	0
17/18	Total number of units	3	10	5	2	3	6	0	5
	Orthodromic	1	2	0	2	1	1	0	1
	Antidromic	1	1	1	0	0	1	0	0
18	Total number of units	41	49	8	16	5	21	6	26
	Orthodromic	9	18	2	2	2	3	0	2
	Antidromic	0	5	0	0	0	0	0	0

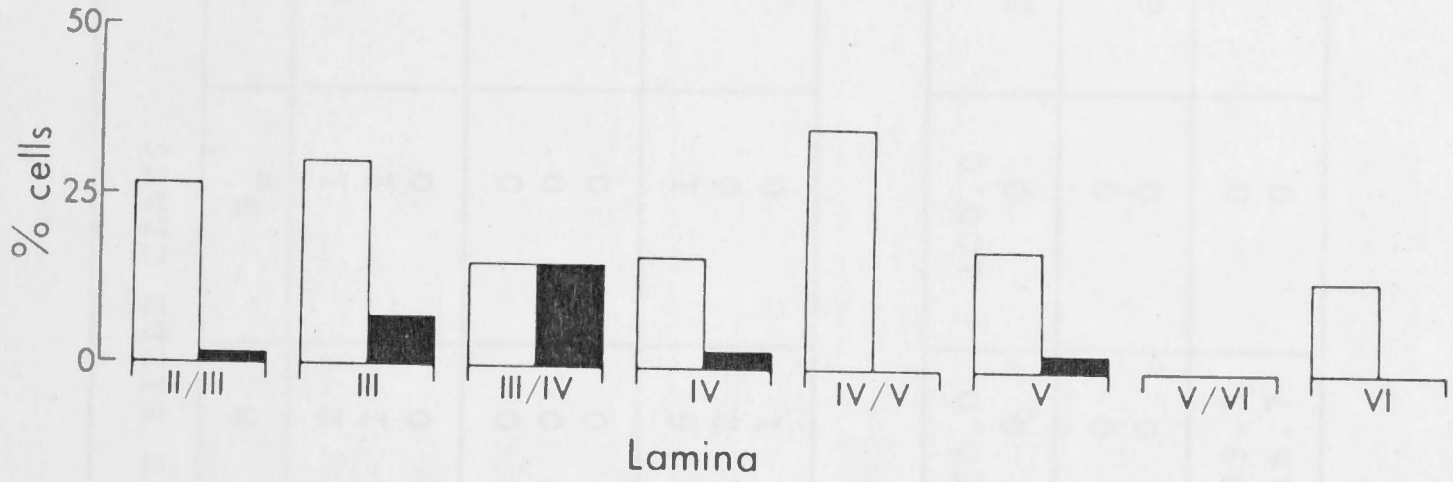


Fig. 10. Proportion of cells in each cortical lamina orthodromically or antidromically activated after electrical stimulation of the corpus callosum and/or contralateral visual cortex. Data pooled from areas 17, 17/18 and 18. Open blocks, orthodromically activated cells; filled blocks, antidromically activated cells.

TABLE 4

Receptive field properties of units activated from CC or CV

(A)

AREA		RECEPTIVE FIELD CLASS								
		S	S_H	C	C_H	B	B_H	A	A_H	Other
17	Number of units	31	20	8	4	2	1	2	1	4
	Orthodromic	3	4	5	2	1	1	0	0	0
	Antidromic	1	2	0	0	0	0	1	0	0
17/18	Number of units	8	4	1	0	0	0	3	0	0
	Orthodromic	3	1	0	0	0	0	0	0	0
	Antidromic	0	1	1	0	0	0	2	0	0
18	Number of units	49	4	21	11	6	1	4	0	1
	Orthodromic	7	1	10	6	2	0	0	0	0
	Antidromic	3	0	0	1	1	0	0	0	0

(B)

17	Orthodromic	9.7	20.0	62.5	50.0	50.0	100.0	0	0	0
	Antidromic	3.2	10.0	0	0	0	0	50.0	0	0
17/18	Orthodromic	37.5	25.0	0	0	0	0	0	0	0
	Antidromic	0	25.0	100.0	0	0	0	66.7	0	0
18	Orthodromic	14.3	25.0	47.6	54.5	33.3	0	0	0	0
	Antidromic	6.1	0	0	9.1	16.7	0	0	0	0

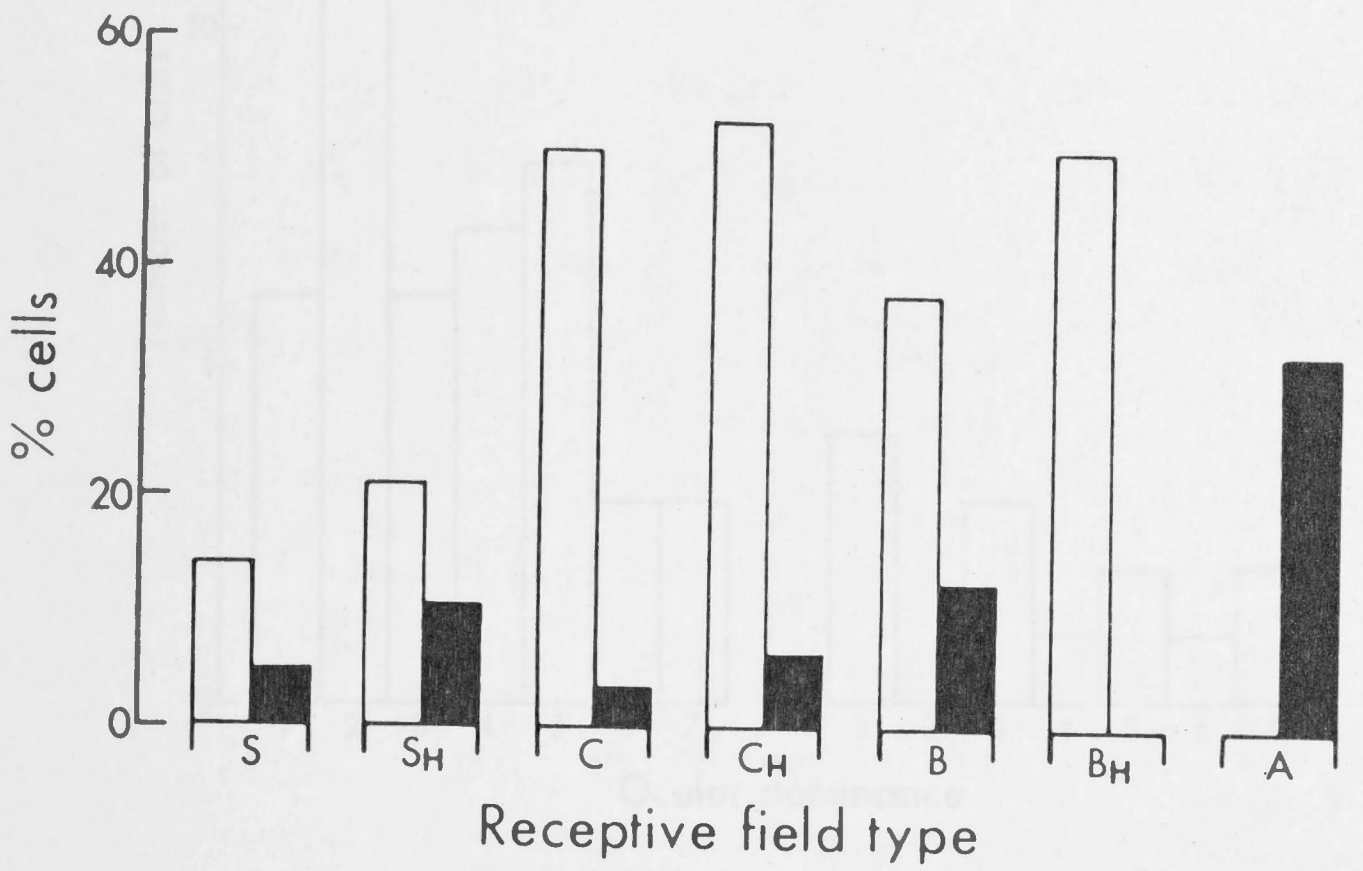
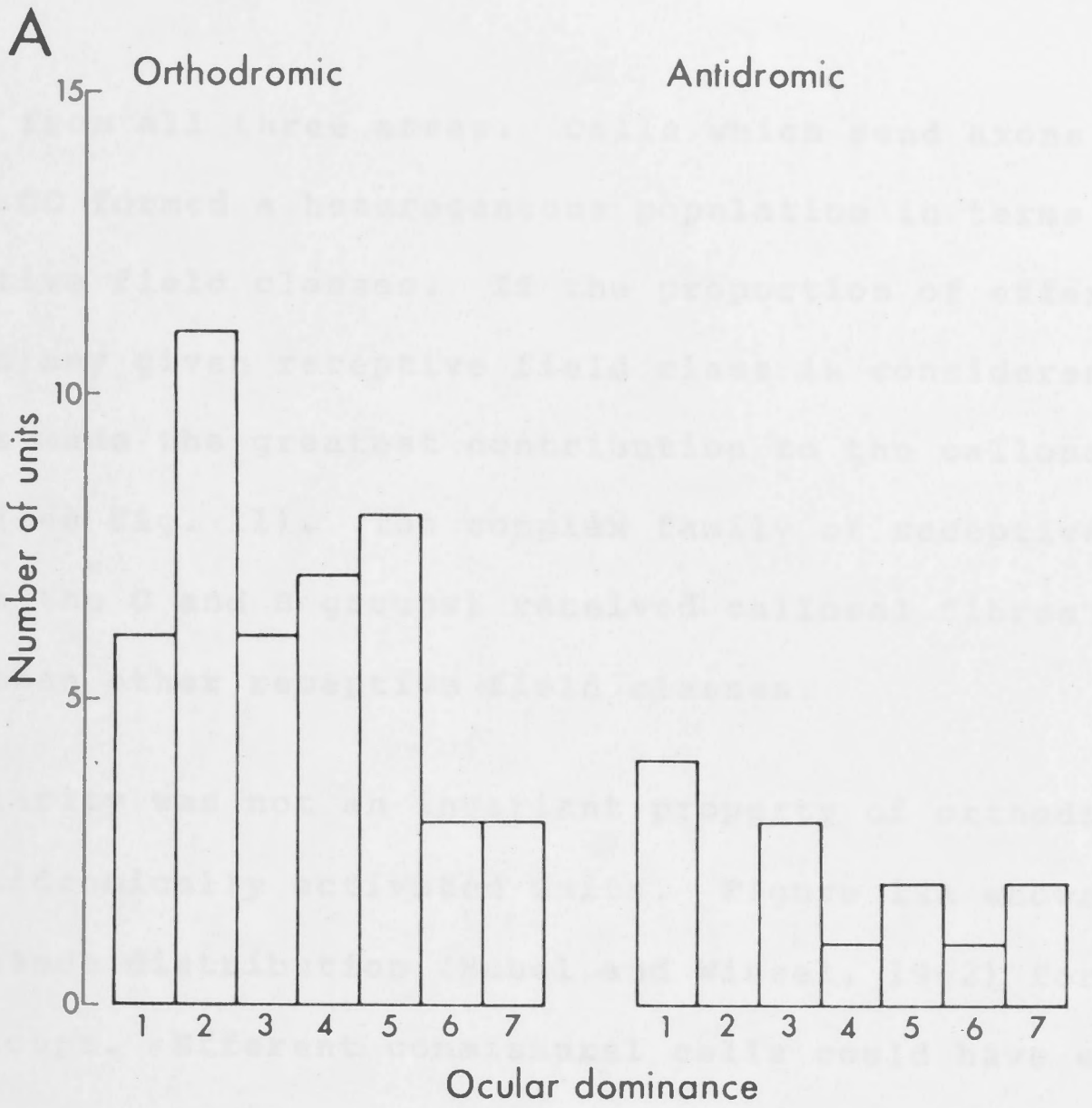


Fig. 11. Proportion of cells in each receptive field class orthodromically or antidromically excited from the corpus callosum and/or contralateral visual cortex. Data pooled from areas 17, 17/18 and 18. Open blocks, orthodromically activated cells; filled blocks, antidromically activated cells.



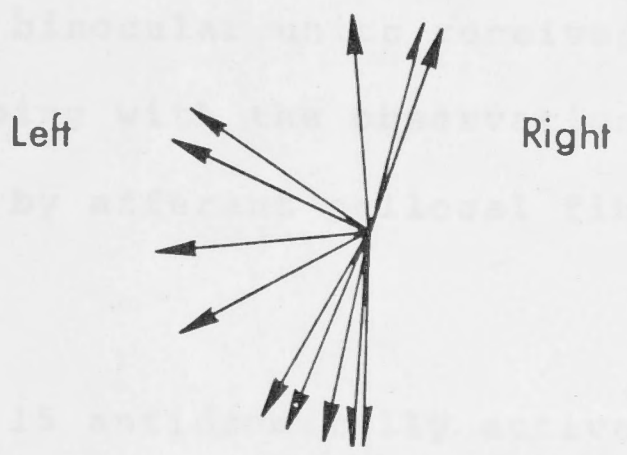


Fig. 12. A: ocular dominance distribution of cells orthodromically and antidromically activated after commissural stimulation. Ocular dominance classes 1 and 7 indicate units driven purely from the contralateral and ipsilateral eyes respectively (Hubel and Wiesel, 1962). B: Optimal direction of stimulus movement for antidromically excited cells. Left, ipsilateral visual field; right, contralateral visual field.

been pooled from all three areas. Cells which send axons through the CC formed a heterogeneous population in terms of their receptive field classes. If the proportion of efferent cells within any given receptive field class is considered, then A cells made the greatest contribution to the callosal projection (see Fig. 11). The complex family of receptive fields (both the C and B groups) received callosal fibres more often than other receptive field classes.

Binocularity was not an invariant property of orthodromically or antidromically activated units. Figure 12A shows the ocular dominance distribution (Hubel and Wiesel, 1962) for these two groups. Efferent commissural cells could have either monocular or binocular receptive fields. In terms of the *total* number of monocular and binocular units in the present study, a higher proportion of binocular units received commissural axons. This is in keeping with the observation that C and B type cells were driven by afferent callosal fibres more often than other cell groups.

Twelve out of the 15 antidromically activated units showed a clear preference for stimulus movement in one direction. The optimal direction of movement for each of these units is shown in Fig. 12B. All efferent units were recorded in the left hemisphere, hence most units preferred movement towards the left, or ipsilateral visual hemifield. Cells in the opposite hemisphere receiving these callosal fibres would thus be commonly driven by stimuli moving into the corresponding contralateral visual field.

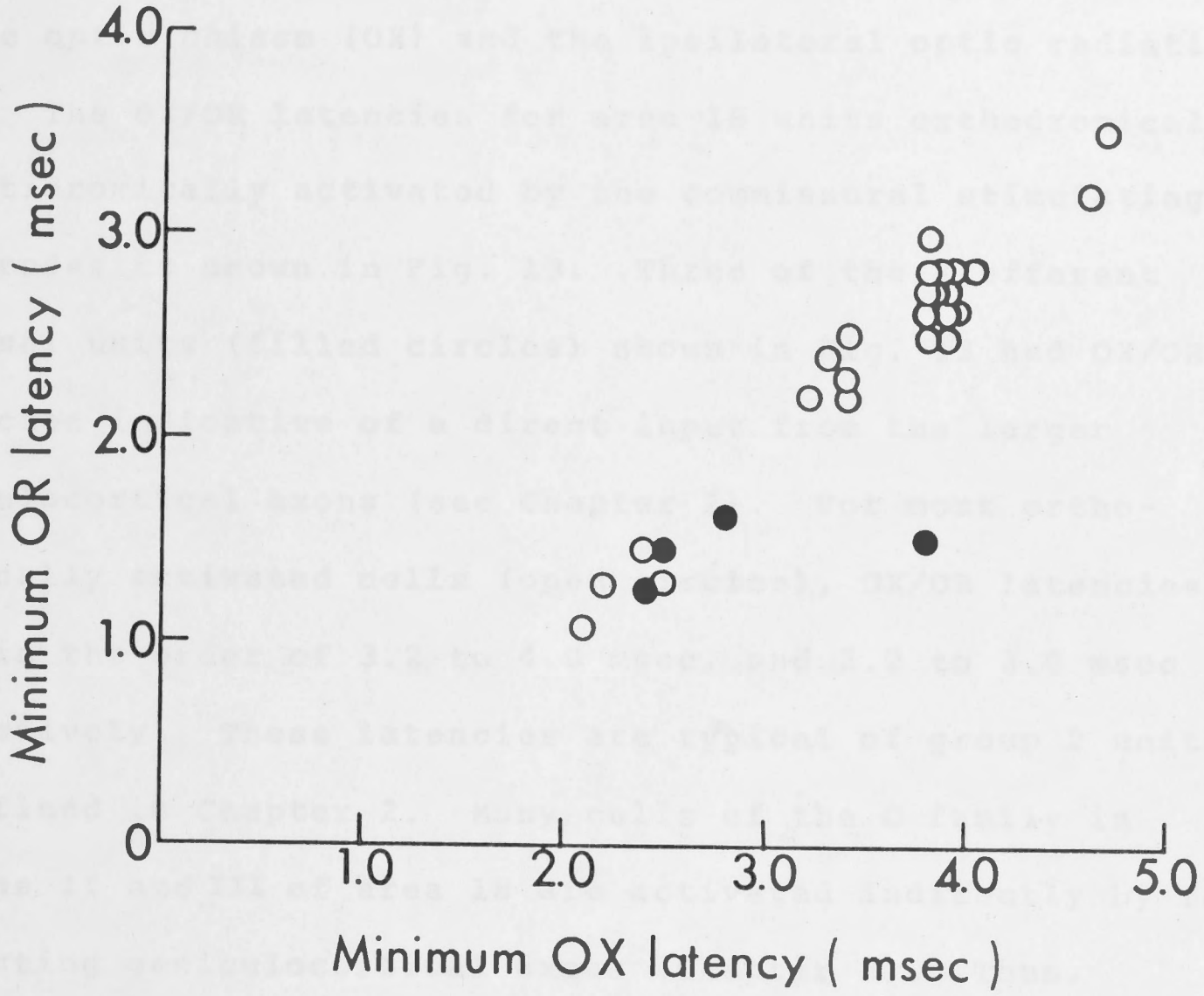


Fig. 13. Orthodromic optic chiasm (OX) and optic radiation (OR) latencies of parastriate cells sending or receiving callosal axons. Open circles, latencies for cells orthodromically excited from the corpus callosum (CC) and/or contralateral visual cortex (CV); filled circles, latencies for cells antidromically activated from CC and/or CV.

Integration of primary and commissural pathways

In some experiments, stimulating electrodes were placed in the optic chiasm (OX) and the ipsilateral optic radiation (OR). The OX/OR latencies for area 18 units orthodromically or antidromically activated by the commissural stimulating electrodes is shown in Fig. 13. Three of the 4 efferent callosal units (filled circles) shown in Fig. 13 had OX/OR latencies indicative of a direct input from the larger geniculocortical axons (see Chapter 2). For most orthodromically activated cells (open circles), OX/OR latencies were in the order of 3.2 to 4.0 msec, and 2.2 to 3.0 msec respectively. These latencies are typical of group 2 units as defined in Chapter 2. Many cells of the C family in laminae II and III of area 18 are activated indirectly by fast conducting geniculocortical axons (Chapter 2). Thus, consistent with the observation that C cells in the superficial laminae received callosal afferents more often than other cell groups, the OX/OR latencies shown in Fig. 13 suggest that cells which received callosal fibres were generally driven indirectly by fast fibres from the ipsilateral dLGN. There were some monocular units which could be orthodromically excited from both the primary *and* callosal pathways. This implies that commissural input need not necessarily give rise to binocularity in cortical cells (see DISCUSSION).

Twenty-four units were antidromically activated from OR and 6 of these units received afferent callosal fibres. Of the 6 cells activated from the callosum, 5 had C type receptive fields and had fast corticofugal axons (mean antidromic latency

to OR stimulation, 0.93 msec). None of the 8 slowly conducting corticofugal S cells (mean OR latency, 9.8 msec) found in the present study, suggested elsewhere as providing the main input to the dLGN (Harvey, 1978 and Chapter 3), could be orthodromically activated from the commissural electrodes.

DISCUSSION

The receptive field properties of splenial fibres and efferent callosal cells recorded in visual cortex : a comparison

Both efferent commissural cells recorded in areas 17 and 18, and callosal fibres recorded in the splenium, had receptive fields close to the vertical midline. This is in agreement with previous reports (Berlucchi *et al.*, 1967; Hubel and Wiesel, 1967; Shatz, 1977a). At both recording sites, a variety of receptive field classes were found to project through the callosum, although significant differences in the two populations are apparent. Firstly, receptive fields of callosally recorded axons were, on average, larger than efferent cells recorded near the 17/18 border. Secondly, 93% of the fibres recorded in the callosum had binocular receptive fields, whereas only 54% of the units recorded near the 17/18 border were binocular. Finally, some spenial fibres had receptive fields typical of more lateral visual areas, but none were found which resembled for example, the S_H cells of area 17 antidromically activated from CC.

Many of the differences noted above are presumably related to the fact the splenial fibres have their origin in a number of visual cortical regions, whereas cortical recording was restricted to the 17/18 border region. The absence of splenial fibres with small receptive fields typical of area 17 may also reflect the inherent difficulties in finding these small fields when there are no indications as to their probable orientation and visual field position. In addition, differences

in splenial and cortical recording may occur if tungsten in glass microelectrodes are biased towards recording from the largest callosal axons.

Bishop and Smith (1964) have claimed that all callosal fibres in the cat are myelinated; most fibres have diameters less than 2μ (the peak is at about 1μ) but fibres could be found as large as 10μ in diameter (cf. their Fig. 3). In the present study, antidromic latencies to CC stimulation ranged from 0.8 to 8.1 msec (mean 1.8 msec). Assuming a conduction distance of 17.5 mm and that conduction velocity approximately equals six times the axon diameter (Hursh, 1939), the diameters of the callosal axons of efferent cells recorded in visual cortex ranged from about 0.4 to 3.6μ, with a mean of 2.2μ. This is in reasonable agreement with the anatomical data of Bishop and Smith (1964),although very short latencies, indicative of the largest callosal axons, were not found. However, there was no tendency for efferent cells in area 17 to have longer antidromic latencies than efferent units in area 18. Thus the absence of splenial fibres with receptive fields typical of area 17 does not seem to be related to the size of striate callosal axons, but is probably due, for the most part, to the difficulties in locating these small receptive fields.

The anatomical distribution of cells which send or receive callosal axons

From the foregoing, there are indications that splenial recording,although useful in providing general information on callosally projecting cells, does not yield a complete account

of the type of visual information being passed from one hemisphere to the other. Further, it is not possible with this technique to identify the exact cortical location of the cells which give rise to, or receive, callosal fibres.

From the histological reconstruction of cortical penetrations, antidromically activated units were found to be located within 1 mm either side of the 17/18 border and the highest proportion of efferent callosal cells was found within the 17/18 border zone itself. These results are in general agreement with previous HRP and electrophysiological studies (Toyama *et al.*, 1974; Innocenti and Fiore, 1976; Shatz, 1977b). Innocenti and Fiore, (1976) found labelled cells up to about 2 mm either side of the 17/18 border and noted that cells were most numerous at the cortical level representing the area centralis. Shatz (1977b) reported that, after unilateral injections of HRP into the 17/18 border at AP positions representing the area centralis, peroxidase filled cells in the contralateral hemisphere were found well into area 18 (see her Fig. 5). All of the penetrations in the present study were made between Horsley-Clark posterior 1 and 5, and receptive fields were mostly within 5^{o} of the area centralis in the inferior visual field. No antidromically activated units were found further than 1 mm into area 18. The presence of HRP-filled cells in area 18, 3 to 4 mm from the 17/18 border (Shatz, 1977b) is surprising since units this distance into area 18 generally have receptive fields about 10^{o} from the vertical midline (see Fig. 7). In agreement with HRP studies (Innocenti and Fiore, 1976; Shatz, 1977b), the

majority of efferent callosal units were located in lamina III, and were found most often in deep III and the III/IV border.

Units receiving callosal fibres, on the other hand, were much more widespread in their anatomical distribution (Fig. 8A and Fig. 10). Although most of these units were located near the 17/18 border, a substantial number were found up to 3 mm into area 18. Most anatomical studies on the termination of callosal fibres do not suggest such a widespread distribution (Hubel and Wiesel, 1967; Fiskin *et al.*, 1975; Shatz, 1977b), however some reports (Garey *et al.*, 1968; Shoumura, 1974; Lund, Mitchell and Henry, 1978) do show some terminal degeneration well into area 18 especially when lesions were made in the cortical locus representing the area centralis. Units orthodromically excited from the callosum were found in all laminae in agreement with anatomical studies (Garey *et al.*, 1968; Jacobson and Marcus, 1970; Fiskin *et al.*, 1975). Some of these anatomical studies (Fiskin *et al.*, 1975; Shatz, 1977b) indicate that the laminar distribution of commissural terminals is different in area 17 and area 18. In the present study, no difference was recognized in the laminar pattern of orthodromically activated units in the two areas.

The receptive field properties of callosally linked cells

Antidromically activated units formed a heterogeneous group in terms of their receptive field classes (Table 4). The same was true for cells which received callosal fibres, although the C and B groups of cells were apparently excited more often

than other receptive field classes (Fig. 11). Hubel and Wiesel (1967) have suggested that complex cells in area 18 with receptive fields which overlap the midline may receive an input from simple cells in the contralateral hemisphere. The observation that many cells in the complex family are orthodromically activated after commissural stimulation could be regarded as supporting this idea. However, S cells are not the only receptive field class which send axons through the corpus callosum; any of the 6 cell types identified as efferent to the callosum could provide the input to the complex-like cells in the contralateral hemisphere. It would be of interest to characterise the receptive fields of simultaneously recorded pairs of units, one in each hemisphere, shown by a technique such as cross correlation analysis to be linked through the callosum. Such an experiment would give clear indications as to how callosally transmitted information is processed and elaborated within the visual cortex.

Integration of primary and callosal visual pathways

Cells sending axons through the callosum were occasionally driven directly by fibres from the ipsilateral dLGN. On the other hand, although cells which *receive* callosal axons were sometimes excited directly by ascending geniculocortical fibres, the majority were activated only indirectly after dLGN stimulation (Fig. 13). The observation that indirectly driven cells of the C and B groups received callosal afferents more often than other cell types is largely in agreement with the reports of Singer *et al.*,(1975) and Tretter *et al.*, (1975), who found that units driven from the dLGN through combined

mono- and polysynaptic or only polysynaptic circuits were commonly excited by callosal afferents. In another study, Toyama *et al.*, (1974) also reported that both Type 1 (monosynaptically excited from the dLGN) and Type 2 (disynaptically excited after dLGN stimulation) neurons received callosal afferents.

EPSPs are elicited monosynaptically and IPSP's disynaptically after commissural stimulation (Toyama *et al.*, 1974). Thus cells receiving callosal fibres will often have the same ordinal position with respect to both the ipsilateral and contralateral dLGN; they are commonly driven indirectly from the ipsilateral dLGN and are monosynaptically activated by efferent cells in the opposite hemisphere which in turn are excited directly by corticogeniculate fibres from their own dLGN.

Units sending axons back into the optic radiation were occasionally excited by commissural stimulation. The majority of these callosally linked units were C cells with fast conducting subcortical axons; these units were probably projecting to the superior colliculus or some part of the thalamus (Singer *et al.*, 1975; Tretter *et al.*, 1975; Chapter 3). No slowly conducting corticofugal S cells were excited by callosal afferents. These cells are likely to send axons to the main laminae of the dLGN (Chapter 3) and it seems that interhemispheric links have little influence on the ipsilateral corticothalamic system. However, Ajmone-Marsan and Morillo (1961) found that stimulation of the *contralateral* gyrus affected the excitability of about one-third of the units

encountered in the dLGN. The anatomical pathways involved in this contralateral influence of the dLGN remain unclear, although it is possible that more extensive searches in lamina VI, near the 17/18 border, would have revealed corticothalamic S cells with callosal input.

The role of the corpus callosum in vision - functional implications of the present analysis

It has been suggested that interhemispheric visual connections subserve a number of visual functions; these include midline stereopsis (Mitchell and Blakemore, 1970), the control of ocular vergence movements (Westheimer and Mitchell, 1969; Blakemore, 1970), and the unification of the two visual hemifields (Choudhury, Whitteridge and Wilson, 1965).

A population of visual cortical neurons with differing receptive field disparities provides the neurophysiological substrate for binocular depth discrimination (Barlow, Blakemore and Pettigrew, 1967; Nikara *et al.*, 1968). However, when an object lies directly behind or in front of a point being fixated, the disparate images of this object fall upon either both nasal or both temporal retinas respectively, hence in each case the two monocular images are projected to opposite cerebral hemispheres. Binocularity in cortical cells coding for midline stereopsis could arise in two ways; either by a direct projection from each eye via the ipsilateral dLGN assuming a certain amount of retina projects to both optic tracts, or if units in the two hemispheres are subsequently interrelated by fibres passing through the corpus callosum.

Evidence supporting the latter suggestion has been reported by Mitchell and Blakemore (1970), who found that a human patient with a sectioned corpus callosum could not judge the depth of objects presented at the midline. In addition, a patient with a sagittally sectioned optic chiasm, who was apparently blind to objects placed behind the fixation point, could see and judge the depths of objects presented in front of the point of fixation (Blakemore, 1970). These results suggest that the callosum is necessary for midline stereopsis; cells which code for these locations in space being binocular due to the convergence of excitatory inputs from the ipsilateral dLGN and the contralateral cortex. In support of this idea, the patient with a split callosum could only make vergence eye movements when both disparate stimuli were peripheral and located in the same visual hemifield. No vergence movements were observed when midline stimuli were presented (Westheimer and Mitchell, 1969).

The conclusions drawn from psychophysical observations have been supported by various physiological studies carried out in cat and monkey. After unilateral section of an optic tract, some cells near the 17/18 border, in the visual cortex ipsilateral to the lesion, could be driven by visual stimuli presented near the vertical midline of the visual field. Responses were abolished by cooling the corresponding points in the contralateral hemisphere and by sectioning the CC (Choudhury *et al.*, 1965; Vesbaesya *et al.*, 1967). In cats with a sagittally sectioned optic chiasm (Berlucchi and Rizzolatti, 1968), some binocular units were recorded close

to the 17/18 border and their monocular receptive fields were always located in corresponding points of the nasal half of the visual field (i.e. temporal retina). Since, after OX section, only fibres from temporal retina reach the visual cortex, the binocularity observed in cortical units must be derived from the integration of the ipsilateral visual pathway with the commissural input from the other hemisphere. Furthermore, Dreher and Cottee (1975) have reported that ablation of parts of areas 17 and 18 significantly reduces the proportion of binocularly driven cells encountered in the corresponding regions of the contralateral hemisphere.

From the present study, it has been shown that geniculo-cortical and commissural fibres do converge on single cells in the visual cortex. However, units which receive this dual projection do *not necessarily* have binocular receptive fields. In order to establish the exact way in which commissural fibres influence cortical neurons, future experiments should perhaps be directed towards studying the binocular interactions of these neurons before and after cooling of the contralateral cortex. With regard to the hypothesis of Blakemore (1969, 1970) concerning the role of the callosum in midline stereopsis, it might be expected that many cells which give rise to callosal fibres would have monocular receptive fields, binocularity only arising in the cell which receives these commissural axons. Recording in the callosum itself has suggested that most callosal axons are *already* binocular (see RESULTS of this paper; Hubel and Wiesel, 1967; Shatz, 1977a). However, from the present study, 6 (45%) of the cortical units antidromically

activated from CC and CV were monocular. Three of these units had S-type receptive fields and could perhaps be involved in the interhemispheric interactions suggested by Blakemore (1969, 1970).

The situation is complicated by the observation that in both cat and monkey, a medial strip of retina does exist which contains both ipsilaterally and contralaterally projecting ganglion cells. Thus a given cerebral hemisphere can receive fibres directly from either both nasal or both temporal retinae. In other words, a portion of visual space in front of and behind the fixation point can be encoded by binocular cortical neurons which derive their input purely from the primary visual projections from the two eyes. In the monkey, this zone is about 1^{o} wide (Stone, Leicester and Sherman, 1973; Bunt, Minckler and Johanson, 1977), hence about 0.5^{o} of the ipsilateral visual field finds representation in the visual cortex. In the cat retina, the crossed-uncrossed division is less clearly defined and the various classes of retinal ganglion cells show different patterns of ipsilateral and contralateral projection (Stone and Fukuda, 1974; Kirk, Levick and Cleland, 1976; Kirk, Levick, Cleland, and Wässle, 1976). The crossed-uncrossed division of X-cells (Stone and Fukuda, 1974) or brisk sustained cells (Kirk, Levick, Cleland and Wässle, 1976) is similar to the pattern already described for the monkey. No ganglion cells more than about 1^{o} into nasal retina have uncrossed axons, however brisk transient cells up to 15.8^{o} in the temporal retina are found to project contralaterally (Kirk, Levick, Cleland and Wässle, 1976), and crossed sluggish

units (Kirk, Levick and Cleland, 1976) or W cells (Stone and Fukuda, 1974) are even more widely distributed in the nasal visual hemifield. All 3 classes of ganglion cell project to the dLGN and visual cortex (Wilson and Stone, 1975; Cleland, Levick, Morstyn and Wagner, 1976; Wilson, Rowe and Stone, 1976; Hollander and Vanegas, 1977; LeVay and Ferster, 1977) although the slowest conducting axons (sluggish or W) do not appear to project to any great extent to areas 17 and 18.

Cortical cells with receptive fields up to about 1.5° in the ipsilateral visual hemifield have been reported (Hubel and Wiesel, 1967; Leicester, 1968; Nikara *at al.*, 1968; Blakemore, 1969; Tusa *et al.*, 1977) and Leicester (1968) has shown that this representation is still present after section of the corpus callosum. The degree of overlap generally found for cortical receptive fields recorded in the two occipital lobes resembles the overlap of crossed-uncrossed X- or brisk sustained ganglion cells in the retina. In the present study, many cortical units had receptive field centres 1 to 2° into the ipsilateral hemifield. Occasionally, however, receptive fields, nearly all of which were driven only from the contralateral eye, were found at much greater distances ipsilateral to the zero vertical meridian (the most peripheral unit was about 13° from the midline). Some of these units were excited after stimulation of OX and OR with latencies indicative of activation by fast (probably brisk transient) geniculocortical axons. This result is not unexpected given that, firstly, brisk transient cells up to 15.8° in temporal retina have crossed retinogeniculate axons (Kirk, Levick, Cleland and Wässle, 1976)

and secondly, receptive field centres of cells up to 36° in the ipsilateral hemifield of the contralateral eye have been found in layer B and the medial interlamina nucleus (MIN) (Kinston, Vadas and Bishop, 1969; Sanderson, 1971; Sanderson and Sherman, 1972; Dreher and Sefton, 1978). Recently it has been shown that both these thalamic areas project to area 18 (cf. Chapter 2).

If brisk transient (Kirk, Levick, Cleland and Wässle, 1976) or Y- (Stone and Fukuda, 1974) fibres from the contralateral and ipsilateral temporal retinae coverge on single cortical neurons, then large disparities could be produced which would code for the depths of objects presented at the midline, independent of the callosum (Levick, 1977). Such binocular units would, however, give no information concerning the depth of objects beyond the fixation point. Cortical units with receptive fields in the ipsilateral eye more than 1 to 1.5° into the ipsilateral hemifield were rarely encountered. This result correlates well with the observation that no ganglion cells with receptive fields more than 1° into the nasal retina are found to project ipsilaterally to the cortex (Stone, 1966; Stone and Fukuda, 1974; Kirk, Levick and Cleland, 1976; Kirk, Levick, Cleland and Wässle, 1976). Thus the perception of depth well beyond the fixation point would seemingly require participation of interhemispheric pathways. One binocular cortical unit had both receptive fields about 4° into the ipsilateral visual hemifield. The unit was orthodromically activated from the callosum and the receptive field from the ipsilateral eye may have been derived from this commissural input, although it should be added that efferent callosal cells

were not found to have such peripheral receptive fields (see below).

Bishop and Henry (1971) have put forward the hypothesis that there are two kinds of steropsis. Fine stereopsis requires closely matched binocular images and operates over a narrow range of spatial disparities. Coarse steropsis is much less specific in that it does not require similar visual stimuli in the two eyes, and can operate up to spatial disparities as much as 7 or 8^{o}. Bishop and Henry (1971) suggest that a population of binocular cortical cells with a range of receptive field disparities, receiving their input from both eyes via the ipsilateral dLGN, provides the receptive field disparity mechanism necessary for fine steropsis. The overlap of crossed-uncrossed X- or brisk sustained cells observed in the retina may well be sufficient to allow binocular units to code for midline steropsis, both in front of and behind the fixation point, independent of the visual callosal fibres coming from the contralateral cortex. Coarse stereopsis, on the other hand, was postulated as requiring transcallosal connections; the stimulus disparities used by Blakemore, (1970) in a patient with OX section, and by Mitchell and Blakemore (1970) in a patient with sectioned callosum, were regarded as being suitable for testing the presence or absence of coarse, and not fine, stereopsis.

In the present study, although efferent callosal units had receptive fields close to the midline, some units receiving commissural fibres had receptive fields up to 9^{o} in the contralateral, and up to 8^{o} in the ipsilateral visual

hemifields. Many of the contralaterally located units were excited by stimulation of the opposite hemisphere which suggests that the cells in the contralateral cortex giving rise to these callosal fibres themselves had receptive fields near the zero vertical meridian. If this is so, then recipient cells would have highly disparate binocular receptive fields, with disparities as large as 10^{o}. This possible range of disparities is very similar to the behavioural limit of 7 or 8^{o} required by coarse stereopsis. Some peripheral units in area 18, activated from CC and CV, had binocular receptive fields but their disparities were always similar to those of other units recorded nearby, which were not excited by commissural stimulation. If the receptive field pairs of peripheral, binocular, callosally excited units are both derived from the primary ipsilateral visual pathway, then the input from the other hemisphere could give rise to another pair of receptive fields near the vertical meridian, making 4 in all. Cells having these properties would be encountered more often in area 18 than in area 17. Large receptive field disparities and units with more than two receptive fields were not found in the present study. However, further quantitative analysis is necessary to investigate these possibilities, since the input from the contralateral hemisphere may be weak, and not recognised using qualitative methods which involve monocular testing of each eye in turn. Lund *et al.*, (1978) have shown that the termination of callosal fibres is modified in cats raised with an induced squint. Unlike normal animals, the callosal projection in these animals extends well into

area 17. Since the callosal system develops comparatively late in development (Anker and Cragg, 1974) it may be that eye alignment is an important factor in determining the distribution of callosal axons (cf. Shatz, 1977a, b). Perhaps the expansion of the callosal projection in cats with induced squint is in some way related to the larger image disparities which must arise from this misalignment.

The callosum is also likely to be involved in unifying the two visual hemifields in order to produce a continuous representation of visual space. In addition, Dow and Dubner (1971) have suggested that callosal connections are important in the visual tracking of objects moving from one hemifield into the other. It might be expected, therefore, that the stimuli of particular relevance in these contexts would generally be those moving towards the vertical boundary between the two hemifields, since only these stimuli would be about to cross from one visual hemifield to the other. Indeed, for efferent callosal units recorded near the 17/18 border, there was a definate tendency for the optimal direction of movement to be towards the ipsilateral visual field (Fig. 12B). This result correlates well with the observations of Dow and Dubner (1971), who found that the callosal input to neurons recorded in the middle suprasylvian gyrus of the cat was specific for movement towards the vertical midline as well as downward. The commissural input to cells in lateral cortical areas with large receptive fields which are not restricted to the contralateral hemifield is likely to provide the physiological basis both for perceptual

unity of visual space and for oculomotor tracking of objects which cross the boundary between the two visual hemifields.

Conclusions

In marked contrast to other corticofugal projections (Chapter 3, Chapter 4), the receptive fields of efferent callosal cells form a remarkably heterogeneous group. This is presumably related to the fact that the callosum is involved in a number of different visual functions. Some significant characteristics of callosally linked units have however, emerged from the present study. Efferent callosal cells have receptive fields close to the vertical midline and tend to have preferred directions of movement towards the ipsilateral visual field. The latter observation may well be related to the role of the callosum in unifying the two hemifields and in alerting the contralateral hemisphere to the fact that an object is about to enter its visual hemifield. Cells receiving callosal axons can have receptive fields well into both the contralateral and ipsilateral visual hemifields. Since the cells of origin of commissural fibres have receptive fields close to the midline, the resulting disparities could provide at least part of the physiological mechanism underlying the perception of large disparate images (coarse steropsis).

The exact nature of the interaction between primary and callosal pathways is not yet clear. In the cat, especially, the observation that substantial parts of the temporal retina contain ganglion cells which project to both ipsilateral and contralateral optic tracts implies that many of the functions

previously ascribed to the callosum do not necessarily require interhemispheric interactions. In monkey, and probably in man, the medial strip from which both crossed and uncrossed axons emerge is only about 1^{o} wide, hence visual callosal connections may be relatively more important in these species.

GENERAL SUMMARY AND CONCLUSIONS

The experiments described in this thesis have examined the functional properties of some of the intrinsic and extrinsic pathways of the cat visual cortex.

Chapters 1 and 2 have examined the afferent connectivity of areas 17 and 18. Cells with S, C and B receptive field properties are found in both regions and in general, the intrinsic organization of the striate and parastriate cortex is very similar. Differences in the functional properties of the various cell types in areas 17 and 18 appear to be related, in the main, to the fact that the afferent input to these areas arises from different cell populations within the lateral geniculate nucleus. Consistent with anatomical studies, the physiological analysis indicates that cells at the bottom of lamina III and in lamina IV are commonly directly driven by geniculocortical fibres. A further afferent input to lamina VI is also described. Although many cell types are monosynaptically innervated, the functional properties of first order neurons in areas 17 and 18 are mostly reflected in the receptive fields of cells in the S family. Some cells in the C and B categories are directly driven, but the majority (especially in area 18) are indirectly activated by thalamic afferents. A model depicting the early stages of afferent processing in area 18 is shown in Fig. 15, Chapter 2.

The physiological analysis supports the cytoarchitectonic subdivision into striate and parastriate cortex and the results indicate that incoming visual information is, for the most part,

processed independently in the two areas. From an examination of the receptive field properties of cells in the two areas, it would seem that each area is capable of discriminating the elements of form and motion of objects in visual space. It is suggested that areas 17 and 18 may be concerned with far and near vision respectively.

The interrelationship of areas 17 and 18 with other cortical and subcortical regions has been examined in Chapters 3, 4 and 5. Consistent with anatomical studies, subcortically projecting neurons are located in laminae V and VI while cells efferent to other cortical areas are found in lamina III. There is a great deal of similarity in the functional properties of striate and parastriate cells projecting to a given extrinsic site. In both areas, C cells in lamina V project to the superior colliculus and thalamic nuclei medial to the lateral geniculate nucleus, while C cells in lamina VI are efferent to the perigeniculate nucleus. The projection from lamina VI to the lateral geniculate nucleus arises from cells with S type receptive fields. The majority of subcortically projecting C cells are indirectly driven by geniculocortical fibres whereas many efferent S cells are monosynaptically excited by incoming afferents. The analysis of the type of visual information being sent to these subcortical regions has been discussed in relation to the possible functional significance of these extrinsic pathways. It is suggested that the C cell projections are involved in general alerting mechanisms, in orienting responses (of both head and eyes) towards novel stimuli and in the first stage of coarse form perception and discrimination. In contrast, the S cell projection is likely to be involved in

high resolution tasks and more static visuomotor behaviours which arise during fixation.

The results in Chapter 4 indicate that the level of processing of visual information attained in the striate cortex prior to transfer to the Clare-Bishop area is mostly reflected in the receptive field properties of B cells. Although there is an apparent homogeneity of function in the tecto-pulvinar-lateral suprasylvian system it is clear that the striate influence on this system is not uniform. Thus C cells project to the superior colliculus and pulvinar complex, whereas B cells are efferent to the Clare-Bishop region. The reason for this distinction has yet to be elucidated.

Unlike the other efferent systems, where a given projection arises from cells with similar receptive field properties, the commissural pathway contains an assortment of cell classes. This presumably reflects the diversity of functions mediated by the interhemispheric system. However, a number of significant characteristics of callosally linked units have emerged and the present results suggest that the callosum is involved in alerting a cerebral hemisphere to the fact that an object is about to enter its visual hemifield and is necessary for the perception of large disparate images (coarse stereopsis).

The afferent projections to areas 17 and 18 from the contralateral cortex and the ipsilateral Clare-Bishop area reveal striking similarities. In both cases the incoming association fibres commonly innervate C and B cells in the superficial layers (II and III) as well as cells located at

the border between lamina IV and lamina V. These results, when considered with the observation that corticocortical projections arise from lamina III, support the concept that the superficial layers are mainly concerned with the intracortical correlation of visual information.

A problem which continually arises in any consideration of the functional importance of connections between one visual are and another is that, despite the anatomical and physiological evidence for these pathways, disruption of a given area often produces little or no observable change in the behavioural responses of an experimental animal. This paradox lies at the heart of the debate concerning functional localization on the one hand and equipotentiality of the visual cortex on the other. Although there are many similarities in the intrinsic organization of areas 17 and 18, there is no doubt that the two areas are physiologically distinct from each other. Furthermore, the apparent normality of animals with lesions confined to specific parts of the visual system may be due to the fact that current behavioural tests are not sufficiently sensitive to recognise any deficits that might occur. There remains, therefore, considerable justification for the proposal that different functions are localised in different regions. However, the richness and complexity of the connections between visual areas implies that the brain functions as a whole, not through the activity of circumscribed areas alone, but by the interplay of its many parts.

A start has been made to study the relative functional importance of individual cortical areas in themselves as compared

to their interrelationships with other visual areas. For the immediate future, the analysis of the response properties and functional connectivity of single cells still appears to be the most effective way of resolving these problems, while at the same time maintaining much of the integrity of the system as a whole.

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.

Albus, K. and Donate-Oliver, F. (1977). Cells of origin of the occipito-pontine projection in the cat: functional properties and intracortical location. *Exp. Brain Res.* 28, 167-174.

Ajmone-Marsan, C. and Morillo, A. (1961). Cortical control and callosal mechanisms in the visual system of cat. *EEG Clin. Neurophysiol.* 13, 553-563.

Anker, R.L. and Cragg, B.G. (1974). Development of the extrinsic connection of the visual cortex in the cat. *J. comp. Neurol.* 154, 29-42.

Baillager, J.-P. (1840). Recherches sur la structure de la *couche corticale* des circonvolutions du cerveau; etc. *Mém. Acad. de méd de Paris*, 8, 148. (Cited by Polyak, 1957).

Baleydier, C. (1977). A bilateral cortical projection to the superior colliculus of the cat. *Neuroscience Letters*. 4, 9-14.

Barlow, H.B., Blakemore, C. and Pettigrew, J.D. (1967). The neural mechanism of binocular depth discrimination. *J. Physiol. (Lond)*. 193, 327-342.

Baumann, T.P. and Spear, P.D. (1977). Role of the lateral suprasylvian area in behavioural recovery from effects of visual cortex damage in cats. *Brain Res.* 138, 445-468.

Berlucchi, G., Gazzaniga, M.S. and Rizzolatti, G. (1967). Microelectrode analysis of transfer of visual information by the corpus callosum *Arch. Ital. Biol.* 105, 583-596.

Berlucchi, G. and Rizzolatti, G. (1968). Binocularly driven neurones in visual cortex of split-chiasm cats. *Science.* 159, 308-310.

Berson, D.M. and Graybiel, A.M. (1978). Parallel thalamic zones in the LP-pulvinar complex of the cat identified by their afferent and efferent connections. *Brain Res.* 147, 139-148.

Bilge, M., Bingle, A., Seneviratne, K.N. and Whitteridge, D. (1967). A map of the visual cortex in the cat. *J. Physiol. (Lond).* 191, 116P.

Bishop, G.H. and Smith, J.M. (1964). The sizes of nerve fibres supplying cerebral cortex. *Exp. Neurol.* 9, 483-501.

Bishop, P.O., Burke, W. and Davis, R. (1962). Single-unit recording from antidromically activated optic radiation neurons. *J. Physiol. (Lond).* 162, 432-450.

Bishop, P.O. and Henry, G.H. (1971). Spatial vision. *Annual Review of Psych.* 22, 119-160.

Bishop, P.O. and Henry, G.H. (1972). Striate neurons: receptive field concepts. *Invest Ophthal.* 11, 346-354.

Bishop, P.O., Henry, G.H. and Smith, C.J. (1971). Binocular interaction fields of single units in the cat striate cortex. *J. Physiol. (Lond).* 216, 39-68.

Bishop, P.O., Kozak, W., Levick, W.R. and Vakkur, G.J. (1962). The determination of the projection of the visual field on to the lateral geniculate nucleus of the cat. *J. Physiol. (Lond).* 163, 503-539.

Blakemore, C. (1969). Binocular depth discrimination and the nasotemporal division. *J. Physiol. (Lond)*. 205, 471-497.

Blakemore, C. (1970). Binocular depth perception and the optic chiasm. *Vision Res*. 10, 43-47.

Brodal, P. (1972a). The corticopontine projection from the visual cortex in the cat. I: The total projection and the projection from area 17. *Brain Res*. 39, 297-317.

Brodal, P. (1972b). The corticopontine projection from the visual cortex in the cat. II: the projection from areas 18 and 19. *Brain Res*. 39, 319-335.

Brodmann, K. (1909). *Vergleichende Lokalisationslehre der Grosshirnrinde in ihren Prinzipien Dargestellt auf Grund des Zellenbaues*. Leipzig : J.A. Barth.

Bunt, A.H., Minckler, D.S. and Johanson, G.W. (1977). Demonstration of bilateral projection of the central retina of the monkey with horseradish peroxidase neuronography. *J. comp. Neurol*. 171, 619-630.

Burrows, G.R. and Hayhow, W.R. (1971). The organization of the thalamo-cortical visual pathways in the cat. *Brain Behav. and Evol*. 4, 220-272.

Cajal, S., Ramón, Y. (1911). *Histologie de Système Nerveux de l'Homme et des Vertebrés, Vol. 2*. Paris. pp.599-618.

Camarda, R. and Rizzolatti, G. (1976a). Receptive fields of cells in the superficial layers of the cat's area 17. *Exp. Brain Res*. 24, 423-427.

Camarda, R. and Rizzolatti, G. (1976b). Visual receptive fields in the lateral suprasylvian area (Clare-Bishop area) of the cat. *Brain Res*. 101, 427-443.

Campbell, A.W. (1904). Histological studies in cerebral localisation. *Brain*. 27, 148-151.

Casagrande, V.A. and Diamond, I.T. (1974). Ablation study of the superior colliculus in the tree shrew *(Tupaia glis)*. *J. comp. Neurol*. 156, 207-238.

Casagrande, V.A., Harting, J.K., Hall, W.C., Diamond, I.T. and Martin, G.F. (1972). Superior colliculus of the tree shrew: a structural and functional subdivision into superficial and deep layers. *Science*. 177, 444-447.

Choudhury, B.P., Whitteridge, D. and Wilson, M.E. (1965). The function of the callosal connections of the visual cortex. *Quart. J. Exptl. Physiol*. 50, 214-219.

Clare, M.H. and Bishop, G.H. (1954). Responses from an association area secondarily activated from the optic cortex. *J. Neurophysiol*. 17, 271-277.

Clarke, E. and O'Malley, C.D. (1968). *The Human Brain and Spinal Cord*. University of California Press. Berkeley and Los Angeles.

Cleland, B.G., Dubin, M.W. and Levick, W.R. (1971). Sustained and transient neurons in the cat's retina and lateral geniculate nucleus. *J. Physiol. (Lond)*. 217, 473-496.

Cleland, B.G., Levick, W.R., Morstyn, R. and Wagner, H.G. (1975). Lateral geniculate relay of slowly conducting retinal afferents to cat visual cortex. *J. Physiol. (Lond)*. 255, 299-320.

Colonnier, M. and Rossignol, S. (1969). On the heterogeneity of the cerebral cortex. In: H.H. Jasper, A.A. Ward and A. Pope (Eds). *Basic Mechanisms of the Epilepsies*, Little, Brown, Boston, Mass., pp.29-40.

Doty, R.W. (1958). Potentials evoked in cat cerebral cortex by diffuse and by punctiform photic stimuli. *J. Neurophysiol.* 21, 437-464.

Dow, B.W. and Dubner, R. (1971). Single-unit responses to moving visual stimuli in middle suprasylvian gyrus of the cat. *J. Neurophysiol.* 34, 47-55.

Dreher, B. (1972). Hypercomplex cells in the cat's striate cortex. *Invest. Ophthal.* 11, 355-356.

Dreher, B. and 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. and Sanderson, K.J. (1973). Receptive field analysis: responses to moving visual contours by single lateral geniculate neurons in the cat. *J. Physiol. (Lond).* 234, 95-118.

Dreher, B. and Sefton, A.J. (In press). Properties of neurones in cat's dorsal lateral geniculate nucleus: a comparison between medial interlaminar and laminated parts of the nucleus. *J. comp. Neurol.*

Dubin, M.W. and Cleland, B.G. (1977). The organization of visual inputs to interneurons of the lateral geniculate nucleus of the cat. *J. Neurophysiol.* 40, 410-427.

Economo, C. (1929). *The cytoarchitectonics of the human cerebral cortex.* Oxford University Press, London.

Fiskin, R.A., Garey, L.J. and Powell, T.P.S. (1975). The intrinsic, association and commissural connections of area 17 of the visual cortex. *Phil. Trans. Roy. Soc. (Lond). B.* 272, 487-536.

Fluorens, P.-J.-M. (1842). *Examen de la Phrénologie*. Paulin, Paris. (Cited by Polyak, 1957).

Garey, L.J. (1971). A light and electron microscopic study of the visual cortex of the cat and monkey. *Proc. Roy. Soc., London, Ser. B.* 179, 21-40.

Garey, L.J., and Blakemore, C. (1977). Monocular deprivation: morphological effects on different classes of neurons in the lateral geniculate nucleus. *Science*. 195, 414-416.

Garey, L.J., Jones, E.G. and Powell, T.P.S. (1968). Interrelationships of striate and extrastriate cortex with the primary relay sites of the visual pathway. *J. Neurol. Neurosurg. Psychiat.* 31, 135-157.

Garey, L.J. and Powell, T.P.S. (1967). The projection of the lateral geniculate nucleus upon the cortex in the cat. *Proc. Roy. Soc. London, Ser. B.* 169, 107-126.

Garey, L.J. and Powell, T.P.S. (1971). An experimental study of the termination of the lateral geniculate-cortical pathway in the cat and monkey. *Proc. Roy. Soc., London, Ser. B.* 179, 41-63.

Gilbert, C.D. (1977). Laminar differences in receptive field properties of cells in cat primary visual cortex. *J. Physiol. (Lond)*. 268, 391-421.

Gilbert, C.D. and Kelly, J.P. (1975). The projections of cells in different layers of the cat's visual cortex. *J. comp. Neurol.* 163, 81-106.

Glickstein, M., King, R.A., Miller, J. and Berkley, M. (1967). Cortical projections from the dorsal lateral geniculate nucleus of cats. *J. comp. Neurol.* 130, 55-76.

Gordon, B. (1973). Receptive fields in deep layers of cat superior colliculus. *J. Neurophysiol.* 36, 157-178.

Graham, J. (1977). An autoradiographic study of the efferent connections of the superior colliculus in the cat. *J. comp. Neurol.* 173, 629-654.

Graybiel, A.M. (1972). Some extrageniculate visual pathways in the cat. *Invest. Ophthal.* 11, 322-332.

Guillery, R.W. (1967). Patterns of fiber degeneration in the dorsal lateral geniculate nucleus of the cat following lesions in the visual cortex. *J. comp. Neurol.* 130, 197-222.

Harvey, A.R. (1978). Characteristics of corticothalamic neurons in area 17 of the cat. *Neuroscience Letters*, 7, 177-181.

Hayashi, Y. (1969). Recurrent collateral inhibition of visual cortical cells projecting to superior colliculus in cats. *Vision Res.* 9, 1367-1380.

Heath, C.J. and Jones, E.G. (1970). Connexions of area 19 and the lateral suprasylvian area of the visual cortex of the cat. *Brain Res.* 19, 302-305.

Heath, C.J. and Jones, E.G. (1972). The anotomical organization of the suprasylvian gyrus of the cat. *Ergebn. Anat. Entwickl. - Gesch.* 45, 4-61.

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

Henry, G.H., Lund, J.S. and Harvey, A.R. (In press). Cells of the striate cortex projecting to the Clare-Bishop area of the cat. *Brain Res.*

Henschen, S.E. (1893). On the visual path and centre. *Brain*. 16, 170-180.

Hoffmann, K.-P. (1973). Conduction velocity in pathways from retina to superior colliculus in the cat: a correlation with receptive-field properties. *J. Neurophysiol*. 36, 409-424.

Hoffmann, K.-P. and Stone, J. (1971). Conduction velocity of afferents to cat visual cortex: a correlation with cortical receptive field properties. *Brain Res*. 460-466.

Hoffmann, K.-P., Stone, J. and Sherman, S.M. (1972). Relay of receptive field properties in dorsal lateral geniculate nucleus of the cat. *J. Neurophysiol*. 35, 518-531.

Hollander, H. (1970). The projection from the visual cortex to the lateral geniculate body (LGB). An experimental study with silver impregnation methods in the cat. *Exp. Brain Res*. 10, 219-235.

Hollander, H. (1972). Autoradiographic evidence for a projection from the striate cortex to the dorsal part of the lateral geniculate nucleus in the cat. *Brain Res*. 41, 464-466.

Hollander, H. (1974). On the origin of the corticotectal projections in the cat. *Exp. Brain Res*. 21, 433-439.

Hollander, H. and 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. and Wiesel, T.N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *J. Physiol. (Lond)*. 160, 105-154.

Hubel, D.H. and Wiesel, T.N. (1965). Receptive fields and functional architecture in two non-striate visual areas (18 and 19) of the cat. *J. Neurophysiol.* 28, 229-289.

Hubel, D.H. and Wiesel, T.N. (1967). Cortical and callosal connections concerned with the vertical meridian of visual fields in the cat. *J. Neurophysiol.* 30, 1561-1573.

Hubel, D.H. and Wiesel, T.N. (1969). Visual area of the lateral suprasylvian gyrus (Clare-Bishop area) of the cat. *J. Physiol. (Lond).* 202, 251-260.

Hursh, J.R. (1939). Conduction velocity and diameter of nerve fibres. *Am. J. Physiol.* 127, 131-139.

Innocenti, G.M. and Fiore, L. (1976). Morphological correlates of visual transformation in the corpus callosum. *Neuroscience Letters* 2, 245-252.

Jacobson, S. and Marcus, E.M. (1970). The laminar distribution of fibers of the corpus callosum: a comparative study in the rat, cat, rhesus monkey and chimpanzee. *Brain Res.* 24, 517-520.

Jacobson, S. and Trojanowski, J.Q. (1974). The cells of origin of the corpus callosum in rat, cat and thesus monkey. *Brain Res.* 74, 149-155.

Joshua, D.E. and Bishop, P.O. (1970). Binocular single vision and depth discrimination. Receptive field disparities for central and peripheral vision and binocular interaction on peripheral single units in cat striate cortex. *Exp. Brain Res.* 10, 389-416.

Kalil, R.E. and Chase, R. (1970). Corticofugal influence on activity of lateral geniculate neurons in the cat. *J. Neurophysiol.* 33, 459-474.

Kato, H., Bishop, P.O. and Orban, G.A. (In press). Hypercomplex and the simple/complex cell classifications in the cat striate cortex. *J. Neurophysiol.*

Kawamura, K. (1973). Corticotectal fiber connections of the cat cerebrum. III. The occipital region. *Brain Res.* 51, 41-60.

Kawamura, S., Sprague, J.M. and Niimi, K. (1974). Corticofugal projections from the visual cortices to the thalamus, pretectum and superior colliculus in the cat. *J. comp. Neurol.* 158, 339-362.

Kelly, J.P. and Van Essen D.C. (1974). Cell structure and function in the visual cortex of the cat. *J. Physiol. (Lond).* 238, 515-547.

Kennedy, H. and Baleydier, C. (1977). Direct projections from thalamic intralaminar nuclei to extra-striate visual cortex in the cat traced with horseradish peroxidase. *Exp. Brain Res.* 28, 133-139.

Kennedy, H. and Magnin, M. (1977). Saccadic influences on single neuron activity in the medial bank of the cat's suprasylvian sulcus (Clare-Bishop Area). *Exp. Brain Res.* 27, 315-317.

Kinston, W.J., Vadas, M.A. and Bishop P.O. (1969). Multiple projection of the visual field to the medial portion of the dorsal lateral geniculate nucleus and the adjacent nuclei of the thalamus of the cat. *J. comp. Neurol.* 136, 295-316.

Kirk, D.L., Levick, W.R., Cleland, B.G. and Wässle, H. (1976). Crossed and uncrossed representation of the visual field by brisk-sustained and brisk-transient cat retinal ganglion cells. *Vision Res.* 16, 225-231.

Kirk, D.L., Levick, W.R. and Cleland, B.G. (1976). The crossed or uncrossed destination of axons of sluggish-concentric and non-concentric cat retinal ganglion cells, with an overall synthesis of the visual field representation. *Vision Res.* 16, 233-236.

Laemle, L.K. (1975). Cell populations of the lateral geniculate nucleus of the cat as determined with horseradish peroxidase. *Brain Res.* 100, 650-656.

Lee, B.B., Cleland, B.G. and Creutzfeldt, O.D. (1977). The retinal input to cells in area 17 of the cat's cortex. *Exp. Brain Res.* 30, 527-538.

Leicester, J. (1968). Projection of the visual vertical meridian to cerebral cortex of the cat. *J. Neurophysiol.* 31, 371-382.

LeVay, S. and 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. and 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. Eng.* 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. and Dubin, M.W. (1972). Lateral geniculate neurons of cat: retinal inputs and physiology. *Invest Ophthal.* 11, 302-311.

Lorente de Nó, R. (1949). Cerebral cortex: architecture, intracortical connections, motor projections. In: J. Fulton. *Physiology of the Nervous System*, Oxford University Press, pp.288-330.

Lund, J.S. (1973). Organization of neurons in the visual cortex, area 17, of the monkey (Macaca Mulatta). *J. comp. Neurol.* 147, 455-496.

Lund, J.S. and Boothe, R.G. (1975). Interlaminar connections and pyramidal neuron organization in the visual cortex, area 17, of the Macaque Monkey. *J. comp. Neurol.* 159, 305-334.

Lund, J.S., Lund, R.D., Hendrickson, A.E., Bunt, A.H. and Fuchs, A.F. (1975). The origin of efferent pathways from the primary visual cortex, area 17 of the macaque monkey as shown by retrograde transport of horseradish peroxidase. *J. comp. Neurol.* 164, 287-304.

Lund, R.D., Mitchell, D.E. and Henry, G.H. (1978). Squint-induced modification of callosal connections in cats. *Brain Res.* 144, 169-172.

Maciewicz, R.J. (1974). Afferents to the lateral suprasylvian gyrus of the cat traced with horseradish peroxidase. *Brain Res.* 78, 139-143.

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

Magalhaes-Castro, H.H., Saraiva, P.E.S. and Magalhaes-Castro, B. (1975). Identification of corticotectal cells of the visual cortex of cats by means of horseradish peroxidase. *Brain Res.* 83, 474-479.

Mason, R. (1975). Cell properties in the medial interlaminar nucleus of the cat's lateral geniculate complex in relation to the transient/sustained classification. *Exp. Brain Res.* 22, 327-329.

Mason, R. (1978). Functional organization in the cat's pulvinar complex. *Exp. Brain Res.* 31, 51-66.

McIlwain, J.T. (1977). Topographic organization and convergence in corticotectal projections from areas 17, 18 and 19 in the cat. *J. Neurophysiol.* 40, 189-198.

McIlwain J.T. and Buser, P. (1968). Receptive fields of single cells in the cat's superior colliculus. *Exp. Brain Res.* 5, 314-325.

Mitchell, D.E. and Blakemore, C. (1970). Binocular depth perception and the corpus callosum. *Vision Res.* 10, 49-54.

Mize, B.R. and Murphy, E.H. (1976). Alterations in receptive field properties of superior colliculus cells produced by visual cortex ablation in infant and adult cats. *J. comp. Neurol.* 168, 393-424.

Munk, H. (1890). Of the visual area of the cerebral cortex, and its relation to eye movements. *Brain* 13, 45-70.

Nelson, J.I., Kato, H. and Bishop P.O. (1977). Discrimination of orientation and position disparities by binocularly activated neurons in cat striate cortex. *J. Neurophysiol.* 40, 260-283.

Niimi, K., Kawamura, S. and Ishimaru, S. (1971). Projections of the visual cortex to the lateral geniculate nucleus and posterior thalamic nuclei in the cat. *J. comp. Neurol.* 143, 279-312.

Niimi, K. and Sprague, J.M. (1970). Thalamo-cortical organization of the visual system in the cat. *J. comp. Neurol.* 138, 219-250.

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

Norton, T.T. (1974). Receptive-field properties of superior colliculus cells and development of visual behaviour in kittens. *J. Neurophysiol.* 37, 674-690.

O'Leary, J.L. (1941). Structure of the area striata of the cat. *J. comp. Neurol.* 75, 131-161.

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

Orban, G.A. and Callens, M. (1977a). Receptive-field types of area 18 neurones in the cat. *Exp. Brain Res.* 30, 107-123.

Orban, G.A. and Callens, M. (1977b). Influence of movement parameters on area 18 neurones in the cat. *Exp. Brain Res.* 30, 125-140.

Otsuka, R. and Hassler, R. (1962). Über Aufbau und Gliederung der corticalen Sehsphäre bei der Katze. *Arch. Psychiat. NervKrankh.* 203, 212-234.

Palmer, L.A. and 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.

Palmer, L.A., Rosenquist, A.C. and Tusa, R.J. (1978). The retinotopic organization of lateral suprasylvian visual areas in the cat. *J. comp. Neurol.* 177, 237-256.

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

Polyak, S. (1957). *The vertebrate visual system.* Ed. H. Kluver. University of Chicago Press.

Remak, R. (1844). Neurologische Erläuterungen. *Arch. Anat. Physiol.* pp. 463-472. (Cited by Clarke and O'Malley, 1968).

Rizzolatti, G. and Camarda, R. (1975). Inhibition of visual responses of single units in the cat visual area of the lateral suprasylvian gyrus (Clare-Bishop area) by the introduction of a second visual stimulus. *Brain Res.* 88, 357-361.

Rizzolatti, G., Tradardi, V. and Camarda, R. (1970). Unit responses to visual stimuli in the cat's superior colliculus after removal of the visual cortex. *Brain Res.* 24, 336-339.

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

Rosenquist, A.C., Edwards, S.B. and 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.

Rosenquist, A.C. and Palmer, L.A. (1971). Visual receptive field properties of cells of the superior colliculus after cortical lesions in the cat. *Exptl. Neurol.* 33, 629-652.

Roucoux, A. and Crommelinck, M. (1976). Eye movements evoked by superior colliculus stimulation in the alert cat. *Brain Res.* 108, 349-363.

Sanderson, K.J. (1971). The projection of the visual field to the lateral geniculate and medial interlaminar nuclei in the cat. *J. comp. Neurol.* 143, 101-138.

Sanderson, K.J., Bishop P.O. and Darian-Smith, I. (1971). The properties of the binocular receptive fields of lateral geniculate neurons. *Exp. Brain Res.* 13, 178-207.

Sanderson, K.J. and Sherman, S.M. (1972). Nasotemporal overlap in the visual field projection to the lateral geniculate nucleus in the cat. *J. Neurophysiol.* 34, 453-466.

Sanides, D., Fries, W. and Albus, K. (1978). The corticopontine projection from the visual cortex of the cat: an autoradiographic investigation. *J. comp. Neurol.* 179. 77-88.

Schmielau, F. and Singer, W. (1977). The role of visual cortex for binocular interactions in the cat lateral geniculate nucleus. *Brain Res.* 120, 354-361.

Shatz, C. (1977a). Abnormal interhemispheric connections in the visual system of Boston siamese cats: A physiological study. *J. comp. Neurol.* 171, 229-246.

Shatz, C. (1977b). Anatomy of interhemispheric connections in the visual system of Boston siamese and ordinary cats. *J. comp. Neurol.* 173, 497-518.

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

Shoumura, K. (1974). An attempt to relate the origin and distribution of commissural fibres to the presence of large and medium pyramids in layer III in the cat's visual cortex. *Brain Res.* 67, 13-25.

Sillito, A.M. (1977a). Inhibitory processes underlying the directional specificity of simple, complex and hypercomplex cells in the cat's visual cortex. *J. Physiol. (Lond).* 271, 699-720.

Sillito, A.M. (1977b). The spatial extent of excitatory and inhibitory zones in the receptive field of superficial layer hypercomplex cells. *J. Physiol. (Lond).* 273, 791-803.

Sillito, A.M. and Versiani, V. (1977). The contribution of excitatory and inhibitory inputs to the length preference of hypercomplex cells in layers II and III of the cat's striate cortex. *J. Physiol. (Lond).* 273, 775-790.

Singer, W. (1970). Inhibitory binocular interaction in the lateral geniculate body of the cat. *Brain Res.* 18, 165-170.

Singer, W., (1977). Control of thalamic transmission by corticofugal and ascending reticular pathways in the visual system. *Physiol. Reviews* 57, 386-420.

Singer, W. and Bedworth, N. (1973). Inhibitory interactions between X and Y units in the cat lateral geniculate nucleus. *Brain Res.* 49, 291-307.

Singer, W., Tretter, F. and Cynader, M. (1975). Organization of cat striate cortex: a correlation of receptive-field properties with afferent and efferent connections. *J. Neurophysiol.* 38, 1080-1098.

Spear, P.D. and Baumann, T.P. (1975a). Receptive field characteristics of single neurons in the lateral suprasylvian visual area of the cat. *J. Neurophysiol.* 38, 1403-1420.

Spear, P.D. and Baumann, T.P. (1975b). Effects of visual cortex removal on receptive field properties of cells in the lateral suprasylvian visual area of the cat. *Neurosci. Abstracts.* 1, 63.

Sprague, J.M., Levy, J., DiBerardino, A. and Berlucchi, G. (1977). Visual cortical areas mediating form discrimination in the cat. *J. comp. Neurol.* 172, 441-488.

Sprague, J.M. and Meickle, Jr., T.H. (1965). The role of the superior colliculus in visually guided behaviour. *Exp. Neurol.* 11, 115-146.

Stein, B.E., Goldberg, S.J. and Clamann, H.P. (1976). The control of eye movements by the superior colliculus in the alert cat. *Brain Res.* 118, 469-474.

Stein, B.E., Magalhaes-Castro, B. and Kruger, L. (1976). Relationship between visual and tactile representations in cat superior colliculus. *J. Neurophysiol.* 39, 401-419.

Sterling, P. and Wickelgren, B.G. (1969). Visual receptive fields in the superior colliculus of the cat. *J. Neurophysiol.* 32, 1-15.

Stone, J. (1966). The nasotemporal division of the cat's retina. *J. comp. Neurol.* 126, 585-600.

Stone, J. and 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.

Stone, J. and Fukada, Y. (1974). The naso-temporal division of the cat's retina re-examined in terms of Y-, X- and W-cells. *J. comp. Neurol.* 155, 377-394.

Stone, J., Leicester, L. and Sherman, S.M. (1973). The naso-temporal division of the monkey's retina. *J. comp. Neurol.* 150, 333-348.

Straschill, M. and Hoffmann, K.-P. (1969). Functional aspects of localization in the cat's tectum opticum. *Brain Res.* 13, 274-283.

Straschill, M. and Rieger, P. (1973). Eye movements evoked by focal stimulation of the cat's superior colliculus. *Brain Res.* 59, 211-227.

Sunderland, S. (1940). The distribution of commissural fibres in the corpus callosum in the Macaque monkey. *J. Neurol. Psychiat.* 3, 9-18.

Syka, J. and Radil-Weiss, T. (1971). Electrical stimulation of the tectum in freely moving cats. *Brain Res.* 28, 567-572.

Talbot, S.A. (1942). A lateral localisation in cat's visual cortex. *Federation Proc.* 1, 84.

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

Tombol, T., Hajdu, F. and Somogyi, G. (1975). Identification of the golgi picture of the layer VI cortico-geniculate projection neurons. *Exp. Brain Res.* 24, 107-110.

Toyama, K., Kimura, M., Shiida, T. and Takeda, T. (1977). Convergence of retinal inputs onto visual cortical cells: II. A study of the cells disynaptically excited from the lateral geniculate body. *Brain Res.* 137, 221-231.

Toyama, K., Maekawa, K. and Takeda, T. (1977). Convergence of retinal inputs onto visual cortical cells: I. A study of the cells monosynaptically excited from the lateral geniculate body. *Brain Res.* 137, 207-220.

Toyama, K. and Matsunami, K. (1968). Synaptic action of specific visual impulses upon cat's parastriate cortex. *Brain Res.* 10, 473-476.

Toyama, K. and Matsunami, K. (1976). Convergence of specific visual and commissural impulses upon inhibitory interneurones in cat's visual cortex. *Neuroscience* 1, 107-112.

Toyama, K., Matsunami, K., Ohno, T. and Tokashiki, S. (1974). An intracellular study of neuronal organization in the visual cortex. *Exp. Brain Res.* 21, 45-66.

Tretter, F., Cynader, M. and Singer, W. (1975). Cat parastriate cortex: a primary or secondary visual area? *J. Neurophysiol.* 38, 1099-1113.

Tusa, R.L., Palmer, R.A. and Rosenquist, A.C. (1978). The retinotopic organization of area 17 (striate cortex) in the cat. *J. comp. Neurol.* 177, 213-236.

Updyke, B.V. (1975). The patterns of projection of cortical areas 17, 18 and 19 onto the laminae of the dorsal lateral geniculate nucleus in the cat. *J. comp. Neurol.* 163, 377-396.

Updyke, B.V. (1977). Topographic organization of the projections from cortical areas 17, 18 and 19 onto the thalamus pretectum and superior colliculus in the cat. *J. comp. Neurol.* 173, 81-122.

Vesbaesya, C., Whitteridge, D. and Wilson, M.E. (1967). Callosal connexions of the cortex representing the area centralis. *J. Physiol. (Lond).* 191, 79-80P.

Wässle, H., Levick, W.R., Kirk, D.L. and Cleland, B.G. (1975). Axonal conduction velocity and perikaryal size. *Exp. Neurol.* 49, 246-251.

Westheimer, G. and Mitchell, D.E. (1965). The sensory stimulus for disjunctive eye movements. *Vision Res.* 9, 749-755.

Wickelgren, B.G. and Sterling, P. (1969). Influence of visual cortex on receptive field properties in the superior colliculus of the cat. *J. Neurophysiol.* 32, 16-23.

Wilson, J.R. and Sherman, S.M. (1976). Receptive-field characteristics of neurons in cat striate cortex: changes with visual field eccentricity. *J. Neurophysiol.* 39, 512-533.

Wilson, M.E. (1968). Cortico-cortical connections of the cat visual areas. *J. Anat. (Lond).* 102, 375-386.

Wilson, M.E. and Cragg, B.G. (1967). Projections from the lateral geniculate nucleus in the cat and monkey. *J. Anat. (Lond).* 101, 677-692.

Wilson, P.D., Rowe, M.H. and Stone, J. (1976). Properties of relay cells in cat's lateral geniculate nucleus: A comparison of W-cells with X- and Y-cells. *J. Neurophysiol.* 39, 1193-1209.

Wilson, P.D. and Stone, J. (1975). Evidence of W-cell input to the cat's visual cortex via the C laminae of the lateral geniculate nucleus. *Brain Res.* 92, 472-478.

Winfield, D.A., Gatter, K.C. and Powell, T.P.S. (1975). Certain connections of the visual cortex of the monkey shown by the use of horseradish peroxidase. *Brain Res.* 92, 456-461.

Wong-Riley, M.T.T. (1974). Demonstration of geniculocortical and callosal projection neurons in the squirrel monkey by means of retrograde axonal transport of horseradish peroxidase. *Brain Res.* 79, 267-272.

Wright, M.J. (1969). Visual receptive fields of cells in a cortical area remote from the striate cortex in the cat. *Nature (Lond).* 223, 973-975.

Yamane, S., Nikara, T. and Sugie, N. (1977). Sustained and transient cortical neurones in area 18 of the cat. *Experentia*, 33, 477-479.