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A PHYSIOLOGICAL ANALYSIS OF SUBCORTICAL AND COMMISSURAL PROJECTIONS OF AREAS 17 AND 18 OF THE CAT

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SUMMARY

1. The corticotectal, corticothalamic and commissural projections of areas 17 and 18 of the cat have been examined using electrical stimulation techniques.

2. In both area 17 and area 18, almost all corticotectal neurones are C cells and have binocular receptive fields. Some of these cells respond equally well to both small moving spots and elongated stimuli, while others only respond to stimuli of restricted length (cf. Palmer & Rosenquist, 1974). Both types are highly direction-selective. A third type of corticotectal C cell responds optimally to long edges or bars and shows only weak direction selectivity. Corticotectal cells generally have fast conducting axons and the majority are encountered in lamina V. About 25% of all cells recorded in lamina V can be antidromically activated from the superior colliculus.

3. Striate and parastriate cells efferent to the thalamus can have either S or C type receptive fields. Corticothalamic S cells are the most common type of efferent cell in lamina VI and have more slowly conducting axons than C cells. Efferent S cells are almost always direction-selective and about half have binocular receptive fields.

4. It is suggested that there may be at least three subgroups within the corticothalamic cells: lamina V C cells project to the pulvinar complex (the same cells may also send axons to the superior colliculus), lamina VI C cells project to the perigeniculate nucleus and lamina VI S cells provide the cortical input to neurones within the lateral geniculate nucleus.

5. In contrast to the corticotectal and corticothalamic projections, the receptive fields of cells projecting through the corpus callosum form a heterogeneous group. All major striate and parastriate receptive field classes are efferent to the contralateral cortex. Their receptive field centres are located close to the vertical mid line and most cells respond best to stimuli moving towards the ipsilateral visual hemifield. Efferent neurones are mostly encountered in lamina III, within about 1 mm either side of the 17–18 border zone.

6. Cells orthodromically excited after commissural stimulation have mostly C or B type receptive fields. Unlike efferent callosal neurones, orthodromically activated cells are encountered up to 3 mm into area 18 and can have receptive fields located up to 9° from the vertical mid line.

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7. The results are discussed with regard to the possible functional significance of each of the corticofugal pathways.

INTRODUCTION

In recent years, improvements in neuroanatomical methods have considerably advanced our knowledge about nerve pathways within the brain. Specifically, the horseradish peroxidase (HRP) technique has been widely used to trace connexions between one region and another, and perhaps more importantly, to identify the neurones which contribute axons to these projections. In the cat, HRP studies have shown that the laminar disposition of efferent cells in visual cortex varies according to the projection site. Neurones in lamina VI of both area 17 and area 18 are efferent to the dorsal lateral geniculate nucleus (d.l.g.n.) (Gilbert & Kelly, 1975; Tombol, Hajdu & Somogyi, 1975) while cells in lamina V send axons to the superior colliculus (Hollander, 1974; Gilbert & Kelly, 1975; Magalhães-Castro, Saraiva & Magalhães-Castro, 1975; Baleydier, 1977), the pontine nuclei (Albus & Donate-Oliver, 1977) and the pulvinar region (Lund, Henry, MacQueen & Harvey, 1979). By contrast, striate and parastriate cells efferent to other cortical areas are mostly located in the supragranular layers (Gilbert & Kelly, 1975; Innocenti & Fiore, 1976; Shatz, 1977; Lund *et al.* 1979). Since the morphological and physiological characteristics of cat visual cortical neurones differ from one layer to the next (e.g. Hubel & Wiesel, 1962; Kelly & Van Essen, 1974; Gilbert, 1977; Henry, Harvey & Lund, 1979; Lund *et al.* 1979) it can be predicted that these differences will be reflected in the response properties of the various types of efferent cell. If this is so, it is of interest to ascertain to what extent these differences are related to the cell's projection site.

The type of visual information transmitted within the corticofugal systems can be assessed directly by analysing the visual properties of single cells shown by electrical stimulation to be efferent to a given subcortical or cortical area. There have been a number of reports (e.g. Palmer & Rosenquist, 1974; Toyama, Matsunami, Ohno & Tokashiki, 1974; Singer, Tretter & Cynader, 1975; Tretter, Cynader & Singer, 1975; Toyama & Matsunami, 1976; Albus & Donate-Oliver, 1977; Gilbert, 1977; Gibson, Baker, Mower & Glickstein, 1978*a*; Henry, Lund & Harvey, 1978; cf. Tsumoto, Creutzfeldt & Legéndy, 1978) which have described the properties of some of these pathways. The aim of the present study is to provide a detailed comparison of the physiological characteristics of corticothalamic, corticotectal and commissurally linked cells in areas 17 and 18 of the cat. The results indicate that the visual properties of efferent cells do indeed vary depending on their projection site and these differences are discussed in relation to the possible functional significance of each of the corticofugal pathways. Analysis of the response characteristics of efferent cells also gives an indication as to the type of physiological and behavioural deficits that might be expected to arise after inactivation of the corticofugal systems. Thus although removal or cooling of visual cortex has marked effects on the response properties of, for example, tectal cells (Wickelgren & Sterling, 1969; Rizzolatti, Tradardi & Camarda, 1970; Rosenquist & Palmer, 1971; Mize & Murphy, 1976), the effects on d.l.g.n. neurones have so far proved less easy to define (Kalil & Chase, 1970; Sanderson, Bishop & Darian-Smith, 1971; Richard, Gioanni, Kitsikis & Buser,

1975; Schmielau & Singer, 1977). The analysis of the commissural pathways has been extended to include a description of orthodromically driven cells, since the properties of these cells differ significantly from those of efferent callosal neurones. Preliminary reports on some aspects of the data described here have been published elsewhere (Harvey, 1976, 1978*a*, *b*).

METHODS

The general methods employed in these experiments have been described in detail elsewhere (Harvey, 1980). Tungsten in glass micro-electrodes (Levick, 1972) were used to record extracellularly from single units in areas 17 and 18 of paralysed cats. The animals were anaesthetized with halothane during all acute surgical procedures and with nitrous oxide supplemented with topical application of local anaesthetics (bupivacaine) during the recording session. The rationale behind this anaesthetic regime and the justification for its use are discussed in the previous paper (Harvey, 1980). All recording electrode penetrations were made between H–C; zero and posterior 5 mm and either passed down the medial bank of the lateral gyrus or were angled to pass tangentially across the border between areas 17 and 18 within the lateral bank of the gyrus. Electrolytic lesions were made at various intervals along the recording penetrations. In many cases, these lesions were placed at the point at which an efferent neurone was isolated (Pl. 1). After perfusion of the animal, 40 μm Nissl-stained sections of the visual cortex were prepared and the electrode tracks reconstructed.

Two types of experiment have been undertaken.

(1) *Subcortical projections*

In order to study the subcortical projections of the striate and parastriate cortex, platinum/iridium glass-insulated stimulating electrodes were placed in the optic radiation, in or close to the d.l.g.n. and in the superior colliculus (s.c.) of twenty cats. Four electrodes were placed in the ipsilateral superior colliculus; two electrodes were positioned at about H–C; anterior 1·5, lateral 1·0 and 3·5 mm, and two were placed at H–C; anterior 4, lateral 1·0 and 3·5 mm. To stimulate as much of the superior colliculus as possible, the system was arranged so that current could be passed between either the posterior or anterior pair as well as between the posterolateral and anteromedial pair of stimulating electrodes. In a number of animals, the s.c. electrodes were used in the recording mode and the background activity was monitored as the electrodes were lowered toward 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 1 or 2 mm from the tectal surface.

Four stimulating electrodes were also placed in the optic radiation (OR). One pair (OR_1) was positioned at approximately H–C; anterior 5·5 to 6·0, lateral 8 and 10 mm, at a depth of about 10 mm. The other pair (OR_2) was placed at H–C; anterior 6·5, lateral 9 and 11 mm, at a depth of about 12·5 mm. The depth of both pairs was adjusted to maximize the evoked cortical response to OR electrical stimulation. The positions of the stimulating electrodes were subsequently verified histologically. The anterior, deep pair was positioned just above or more commonly, just within the d.l.g.n. In addition to the above arrays, a pair of stimulating electrodes was also placed in the optic chiasm (OX) (cf. Harvey, 1980) in order to examine the afferent connectivity of subcortically projecting cells. Only those cats in which antidromic activation could be elicited at low thresholds (1–10 V) from both the s.c. and OR electrodes are included in the present analysis.

(2) *Commissural projections*

In the second part of the study, stimulating electrodes were placed in the corpus callosum (c.c.) and contralateral visual cortex (c.v.) in order to investigate the commissural connexions of areas 17 and 18. In four cats only c.c. electrodes were present and in sixteen animals both c.c. and c.v. electrodes were used. As above, electrodes were also occasionally placed in the optic chiasm and ipsilateral optic radiation. For callosal stimulation, a linear array of four electrodes, each 2 mm apart, was stereotaxically positioned between H–C; anterior 2 mm and 8 mm,

about 1·5 mm lateral to the mid line, contralateral to the recording hemisphere. From experiments in which fibres were recorded from the splenium of the corpus callosum itself (A. R. Harvey, unpublished observations), 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 splenial pair of electrodes always had the lowest thresholds and the most anterior pair the highest.

The number of stimulating electrodes placed in the contralateral cortex varied from 6 to 9. The electrodes were arranged to be in a corresponding position to the site of recording in the contralateral hemisphere. In most experiments, three pairs of stimulating electrodes were positioned at approximately H–C; zero, posterior 2·5 mm and posterior 5 mm. The lateral and medial electrodes of each pair were inserted to a depth of 1 or 2 mm in the lateral and medial banks of the lateral gyrus respectively. The 17–18 border could be stimulated by five different electrode pairs. A third array of stimulating electrodes was sometimes placed more laterally in area 19. As in other experiments, the exact positions of the c.c., c.v., OX and OR stimulating electrodes were checked histologically, either by gross dissection or more usually by examination of 40 μm Nissl-stained sections.

The criteria used to distinguish antidromic from orthodromic activation were based on those of Bishop, Burke & Davis (1962). The main test used was that of impulse collision, examples of which are shown in Figs. 3 and 4 (cf. Harvey, 1978*a*). Conduction of an antidromically evoked spike can be blocked by a visual or spontaneous orthodromic spike elicited in the cell body prior to electrical stimulation, whenever the time difference between the orthodromic spike and electrical stimulation is less than the antidromic latency. Antidromic invasion was confirmed by observing the fractionation of the wave form of the action potential at high rates of stimulation and the fixed latency of response of electrically evoked spikes. Impulses elicited trans-synaptically by electrical stimulation cannot be collided with a spontaneous or visually evoked orthodromic action potential since this latter spike travels along an axon different from the one being stimulated. In addition, electrically evoked orthodromic spikes do not normally follow high frequencies and often have considerable variability in their latencies (cf. Harvey, 1980). Note, however, that trans-synaptic activation does not necessarily result from orthograde activation of an axon projecting into the cortex and innervating a cell. A neurone may also be so activated if it is innervated by the recurrent collateral of an axon of a nearby cell which is itself projecting out of the cortex and is antidromically activated after electrical stimulation. This ambiguity is of particular relevance in the commissural study, and it should be pointed out that some of the cells orthodromically excited after commissural stimulation may be activated via recurrent fibres.

A further problem which arises if both the afferent and efferent pathway to and from a cell are excited from the same stimulating electrodes is that after a single electrical shock, antidromic spikes will only be recorded at the soma if the afferent pathway has a longer latency than the efferent path. If an afferent spike arrives first, the cell will itself send an orthodromic action potential along its axon which will collide with the more slowly conducting antidromic spike. As a result, antidromic action potentials will not be recorded at the cell body. This is of particular importance in the corticothalamic experiments since many lamina VI efferent cells have slowly conducting axons. In practice, very few long latency efferent cells in area 17 were orthodromically excited after OR stimulation. Of those that were, most were only driven when the electrical shock followed closely after a naturally occurring spike (A. R. Harvey, in preparation) at a time when collision of the antidromic spike had already occurred. In area 18, where many more cells were orthodromically activated from OR, afferent spikes were eliminated by high frequency stimulation in order to see if longer, fixed-latency spikes then became apparent. Further, orthodromic spikes were sometimes elicited from only one pair of OR stimulating electrodes while antidromic spikes were evoked from the other or both pairs. The thresholds of orthodromic and antidromic spikes also varied from one stimulating site to another.

The laminar patterns of areas 17 and 18, and the location of the border between these two areas were identified in Nissl-stained preparations using established criteria (O'Leary, 1941; Otsuka & Hassler, 1962; Garey, 1971; Lund *et al.* 1979; cf. Harvey, 1980). Lamina IV of both area 17 and area 18 has not been subdivided in the present analysis. The cytoarchitectonic criteria used to define the 17–18 border in the present study are outlined below:

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

(2) 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.

(3) 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 it was not possible to identify an exact point at which area 17 stopped and area 18 began. Rather, there appeared to be a zone, 150–250 μm 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 Pl. 2. The two dotted lines indicate the limits of the transition area.

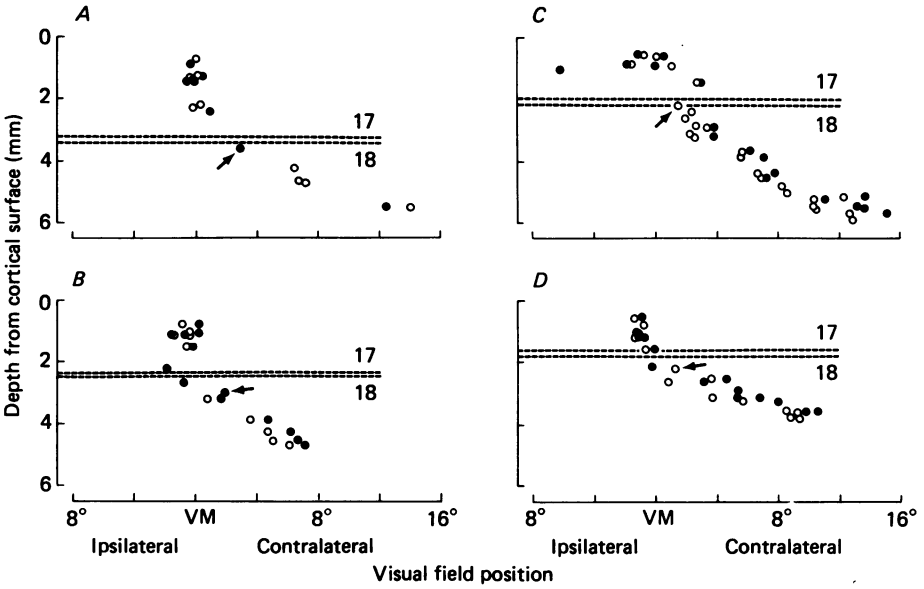

Fig. 1. *A*–*D*: Four micro-electrode penetrations through the lateral bank of the lateral gyrus. The visual field location of the receptive field centres of cortical units are plotted against the depth these units were encountered from the cortical surface. In each graph, the extent of the 17–18 border zone is shown by the two dashed lines. Arrows indicate first unit regarded as having receptive field properties characteristic of area 18. Filled circles, right (contralateral) eye; open circles, left (ipsilateral) eye; VM, vertical mid line.

Area 17 is above the zone, and area 18 below. There is a consistent correlation between the histologically defined border zone and the transition from area 17 to area 18 as derived from physiological recording. In Fig. 1 the visual field position of single units recorded in four electrode penetrations which passed through the lateral bank of the lateral gyrus is related to the cyto-architectonically defined border zone. The arrow in each plot indicates the first cell regarded as having receptive field properties characteristic of area 18. The first physiologically classified area 18 unit is always found close to the histologically identified 17–18 border zone. In addition, it is clear that receptive fields only start to move away from the vertical mid line when penetrations enter area 18. In most of the following analysis, units located within the 17–18 border zone have been placed in a separate group from those definitely located in area 17 and area 18.

In all experiments, receptive fields were plotted using hand-held visual stimuli. Cells were classed as S, C, B or A, using criteria described elsewhere (Henry, 1977; Henry *et al.* 1978; Henry *et al.* 1979; Harvey, 1980). End-zone inhibition was sometimes present in all of the above receptive field classes and these cells have been designated S_H, C_H, B_H and A_H.

RESULTS

Part 1

Corticotectal and corticothalamic projections

Electrical stimulation of the corticotectal and corticothalamic pathways was tested on 415 units isolated in areas 17 and 18. Seventy-nine (19%) of these cells were antidromically activated from one or more of the subcortical stimulating sites. Fifty of these corticofugal units were in area 17, 23 in area 18 and 6 were located within the 17–18 border zone. Thirty-four cells were activated from the superior colliculus of which thirty-two were also driven from the OR. The observation that many corticocollicular units are driven from the OR electrodes is consistent with anatomical studies which indicate that corticotectal fibres pass close to the d.l.g.n. on their way to the colliculus (Garey, Jones & Powell, 1968). The remaining forty-five corticofugal cells were activated after stimulation of the optic radiation but could not be excited from the tectum. Twenty-four of these neurones were excited from both OR stimulating sites, seven were driven only from the anterior pair and fourteen were activated exclusively from the posterior electrodes. In other words, thirty-one of the corticofugal cells not stimulated from the tectum were antidromically excited from the stimulating electrodes placed just above or more typically just within the d.l.g.n. For brevity, cells excited from OR but not from the tectum will be described as corticothalamic in the remainder of this analysis. The destination of these corticofugal fibres will be considered further in the Discussion.

Receptive field properties of corticotectal and corticothalamic neurones

Corticotectal neurones. Twenty-nine of the corticotectal neurones could be classed according to their responses to visual stimuli. *All* of these cells were classed as C cells (cf. Palmer & Rosenquist, 1974; Singer *et al.* 1975; Tretter *et al.* 1975). Seventeen were in area 17, 9 in area 18 and 3 were located within the 17–18 border zone. Corticocollicular cells had superimposed light and dark edge response regions when tested with moving stimuli and gave a composite ON/OFF discharge to flashing stimuli. They were broadly tuned for stimulus orientation and on average continued to respond to stimuli inclined up to 50° from the optimal. Corticotectal cells in area 18 were in general more broadly tuned than their counterparts in the striate cortex. Corticocollicular neurones had a relatively high spontaneous discharge (5–20 Hz) and 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.

Palmer & Rosenquist (1974) have reported that the majority of corticotectal units lack any clear summation along the line of optimal orientation and respond equally well to both small moving spots and elongated stimuli. In the present study, qualitative testing revealed that although many corticocollicular cells were similar to those described by Palmer & Rosenquist (1974), a significant number did not respond to small stimuli but were optimally excited by longer (2° or more) edges or bars. In agreement with Palmer & Rosenquist (1974), the response of a small number of efferent C cells was inhibited by long edges and these cells showed clear end-zone inhibitory regions (C_H cells). The number of corticocollicular cells of each type are shown in Table 1. In total, twenty-two corticotectal C cells were tested with stimuli

of various lengths; ten resembled the Palmer & Rosenquist cell, four were C_H and eight preferred elongated stimuli.

Six corticotectal neurones responded equally well to optimally oriented stimuli moved in either direction. The remainder (twenty-three: 79 %) showed various

TABLE 1. Receptive field properties of corticotectal neurones

	Area		
	17	17–18	18
C Palmer & Rosenquist type	7	0	3
Responsive to long edges	4	2	2
End-stopped (C_H)	2	0	2
Not tested	4	1	2
Not classified	4	0	1

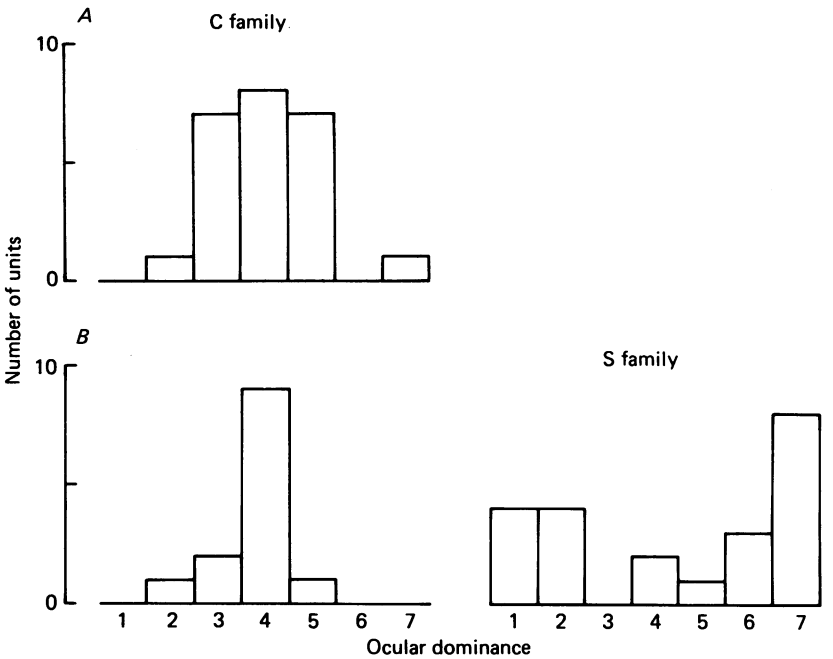

Fig. 2. Ocular dominance distributions of corticotectal and corticothalamic cells. *A*: cells antidromically activated from the superior colliculus; *B*: cells antidromically activated only from the optic radiation. Ocular dominance expressed on a scale ranging from 1 (driven solely from contralateral eye) to 7 (driven solely from ipsilateral eye) (cf. Hubel & Wiesel, 1962). Data pooled from areas 17 and 18.

degrees of directional specificity. Seventeen of these units were completely, or almost completely, direction-selective in that movement in the non-preferred direction evoked no or only minimal response. Of the ten C cells which showed little or no length summation, nine were highly selective for the direction of stimulus movement. In contrast, of the eight C cells which responded optimally to long edges, four showed no direction specificity and two were only weakly selective. These results suggest

that there is a relation between the degree of length summation and the amount of direction selectivity in corticotectal neurones.

The ocular dominance distribution of corticocollicular cells is shown in Fig. 2*A*. It was not possible to assess accurately the ocular dominance of five corticotectal neurones but all had binocular receptive fields. In total therefore, twenty-eight of the twenty-nine visually characterised corticocollicular units in areas 17 and 18 were binocularly discharged by visual stimulation. The majority of these binocular cells

TABLE 2. Receptive field properties of corticothalamic neurones

		Area		
		17	17–18	18
S		19	0	6
C	Palmer & Rosenquist type	3	1	1
	Responsive to long edges	1	1	1
	Not tested	2	0	3
Not classified		4	1	2

were driven about equally by the two eyes. This result is very much in agreement with that of Palmer & Rosenquist (1974). The major difference between striate and parastriate corticocollicular C cells is the size of the receptive fields; the mean area of the receptive fields of area 17 corticotectal neurones is 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° of the area centralis, this difference is not related to the eccentricity of striate and parastriate neurones. The receptive fields of corticotectal cells in both visual areas are generally larger than the fields of other cells at corresponding eccentricities.

Corticothalamic neurones. The receptive fields of thirty-eight of the forty-five corticothalamic neurones were analysed. Twenty-five of these cells were located in area 17, eleven in area 18 and two within the 17–18 border zone. The number of corticothalamic cells of each receptive field type found in each cortical area are shown in Table 2.

S cells have spatially separate response regions to moving light and dark edges, and, when responsive to flashing stimuli, can be subdivided into separate ON and OFF areas. They were the most frequently encountered corticothalamic neurone in both areas 17 and 18, comprising 76% and 55% of all visually classified corticothalamic cells in the striate and parastriate cortex respectively. Efferent S cells in both areas were sharply tuned for stimulus orientation and most ceased to respond when the stimulus was angled more than 30° from the preferred orientation. Corticothalamic S cells generally had no or only low spontaneous activity 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. Gilbert (1977) has reported that the receptive fields of striate simple cells in lamina VI are much longer than those in lamina IV. Although length response curves were not determined in the present study, it is perhaps significant that most efferent S cells, especially in area 17, responded poorly

to a small spot flashed within the receptive field or moved in the preferred direction through the receptive field. Furthermore, the length of efferent S cell receptive fields as determined from the minimum-response field commonly had a negative dimension in that the lateral borders were often overlapped or crossed with respect to each other. These results suggest that corticofugal S cells require substantial summation along the length of the receptive field.

An 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, eighteen of the nineteen corticothalamic S cells were completely or almost completely selective for the direction of movement of an optimally oriented stimulus. In total, forty-two S cells recorded at the border between laminae V and VI and in lamina VI itself showed marked directional specificity; hence 43 % of these units (eighteen of forty-two) were antidromically activated from the optic radiation. In contrast, only one of the eight (12 %) layer VI S cells which exhibited no, or only weak, direction selectivity had a corticothalamic axon. The pattern is very similar in area 18. Of the twelve S cells in lamina VI which were completely or almost completely direction-selective, six (50 %) were antidromically activated, whereas none of the four weakly direction-selective neurones in this layer had efferent axons.

The ocular dominance distribution of corticothalamic striate and parastriate S cells is shown in Fig. 2*B*. Out of the twenty-two cells for which ocular dominance could be satisfactorily determined, twelve (55 %) had monocular receptive fields. It should be pointed out that the ocular dominance distributions described above relate only to the excitatory component in the cell's response. Indeed, in four efferent S cells with apparently monocular receptive fields, it was possible to detect an influence from the non-dominant eye when both eyes were stimulated simultaneously. In three cases, the predominant effect appeared to be inhibitory and in the other, the effect was facilitatory.

Thirteen C cells were antidromically activated from the stimulating electrodes in the optic radiation but were not driven from the superior colliculus (Table 2). Five of these cells resembled the Palmer & Rosenquist (1974) cell and three others fired optimally to elongated stimuli. Nine of the thirteen C cells were completely or almost completely direction-selective. Like corticocollicular cells, corticothalamic C cells commonly had high spontaneous activity, were broadly tuned for stimulus orientation and continued to respond at high stimulus velocities. The ocular dominance distribution of these C cells is shown in Fig. 2*B*. The binocularity of corticothalamic C cells is in marked contrast to the high degree of monocularity exhibited by efferent S cells.

Antidromic latencies of corticotectal and corticothalamic cells

Examples of antidromic activation of a corticotectal C cell and a corticothalamic S cell are shown in Figs. 3 and 4. The C cell was in layer V of area 17 and had OR and s.c. latencies of 1·5 and 2·4 msec respectively. The S cell was in lamina VI of area 17 and was activated at a latency of 18·0 msec after stimulation from the posterior OR electrodes. Fig. 5 compares the antidromic OR latencies of corticocollicular and corticothalamic neurones in areas 17 and 18. Cells in the C family (C and C_H cells), whether or not they are projecting to the tectum, generally have more rapidly

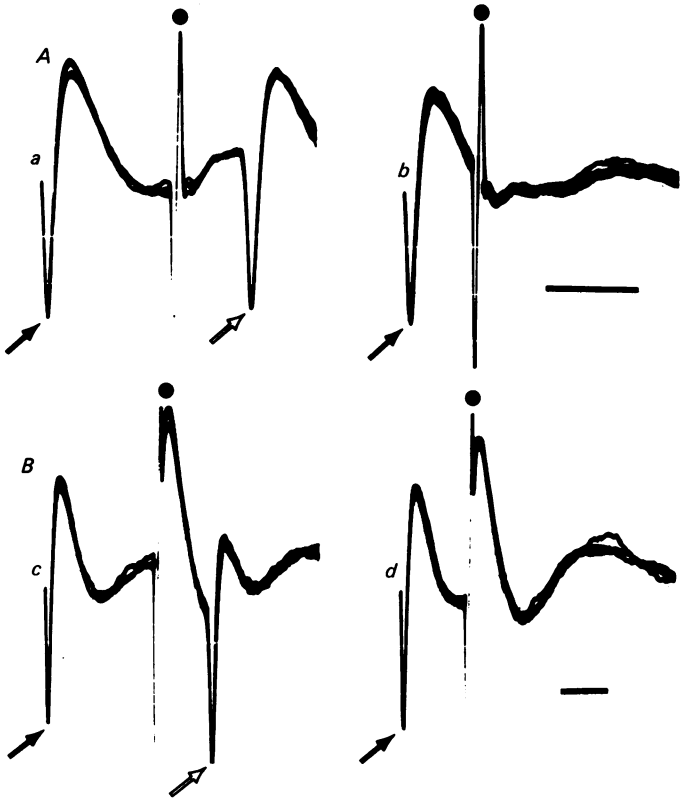

Fig. 3. Antidromic activation of a C cell in lamina V of area 17. *A*: electrical stimulation of optic radiation (*a*), collision (*b*) of antidromic spike; *B*: electrical stimulation of superior colliculus (*c*), collision (*d*) of antidromic spike. Filled arrow, orthodromic spike; open arrow, antidromic spike; filled circle, stimulus artifact. *A*, *B*: time marker, 2 msec.

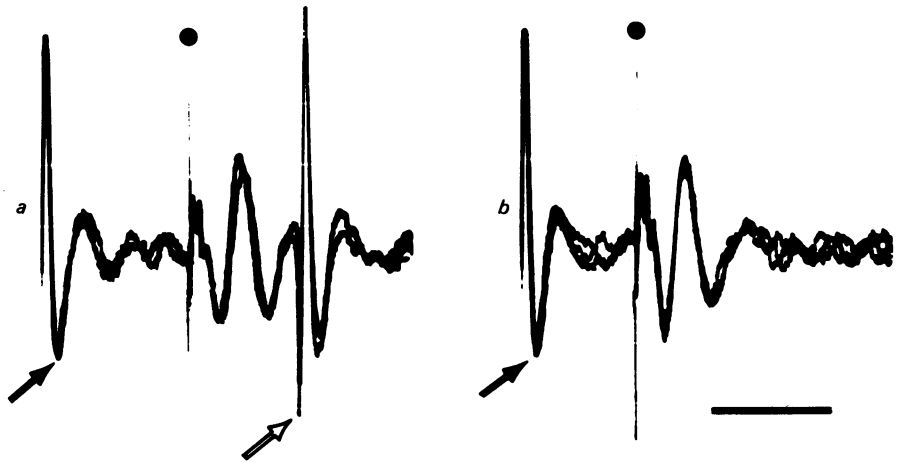

Fig. 4. Antidromic activation of an S cell in lamina VI of area 17 after stimulation from the posterior optic radiation (OR_1) electrodes (*a*). This cell was also excited from the anterior (OR_2) electrodes. Collison of antidromic spike (*b*). Filled arrow, orthodromic spike; open arrow, antidromic spike; filled circle, stimulus artifact. Time marker, 20 msec.

conducting axons than corticothalamic S cells. This is true for both area 17 and area 18. The mean OR latencies for striate and parastriate corticotectal neurones are 1·1 and 1·5 msec respectively, while the mean latencies for corticothalamic C cells in areas 17 and 18 are 1·1 and 1·0 msec. In comparison, the mean antidromic latency for efferent S cells is 6·5 msec in both area 17 and area 18. With regard to the cells projecting to the superior colliculus, the mean s.c. latency for all thirty-four corticotectal cells is 2·6 msec with a range of 1·2 to 7·8 msec. This mean is very similar to

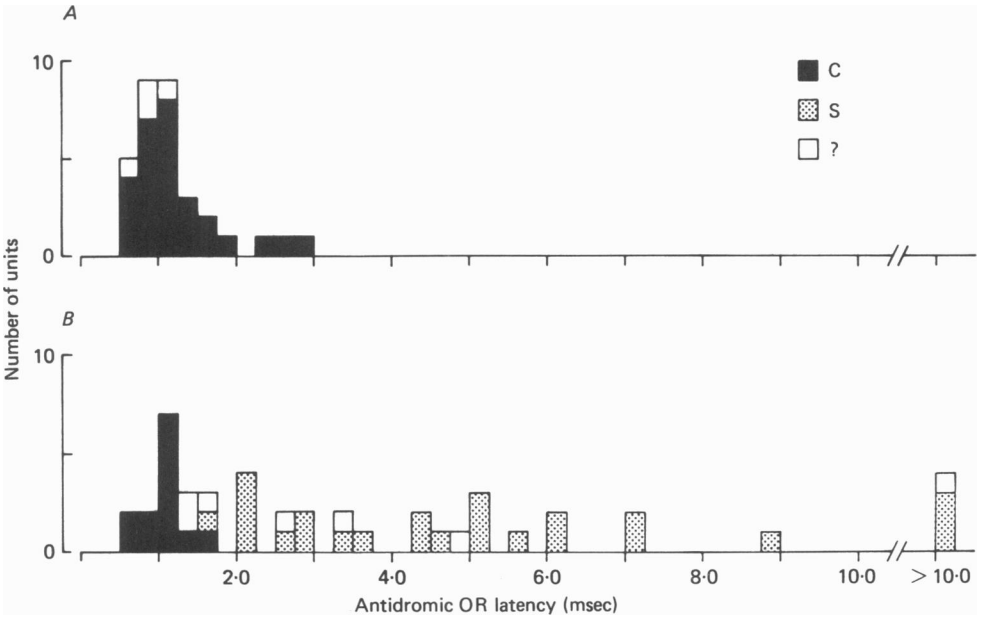

Fig. 5. Antidromic latencies of corticotectal and corticothalamic neurones obtained after electrical stimulation of the optic radiation. *A*: cells activated from the superior colliculus; *B*: cells activated only from the optic radiation. Filled blocks, cells in the C family; stippled blocks, S cells; open blocks, unclassified cells. Data pooled from areas 17 and 18.

that of 2·3 msec reported by both Palmer & Rosenquist (1974) and Toyama *et al.* (1974) and of 2·8 msec reported by Hayashi (1969). Thirty-two corticotectal neurones were antidromically activated from the superior colliculus and also from the optic radiation (which resulted in a shorter latency); the latency differences between these varied from 0·6 to 5·4 msec. Given that the distance from the OR to the s.c. stimulating electrodes is about 12–15 mm, these differences indicate that the conduction velocity of corticotectal fibres ranges from about 2 to 20 m/sec. Despite this broad range of velocities, the majority of corticocollicular neurones give rise to fast conducting fibres and most of the information from the cortex reaches the colliculus in less than 3 msec.

It has been suggested (e.g., Guillery, 1967) that the fine axons within the d.l.g.n. which degenerate after cortical lesions may be collaterals of coarser corticofugal fibres. Fig. 6 presents the antidromic latencies for corticothalamic neurones stimulated from both the posterior (OR_1) and anterior (OR_2) electrode pairs. The dashed line represents what would be expected if the two pairs were in the same position

and the continuous 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 increase in the OR_1–OR_2 difference for long latency corticothalamic axons (all of which originated from cells in lamina 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. One S cell, not shown

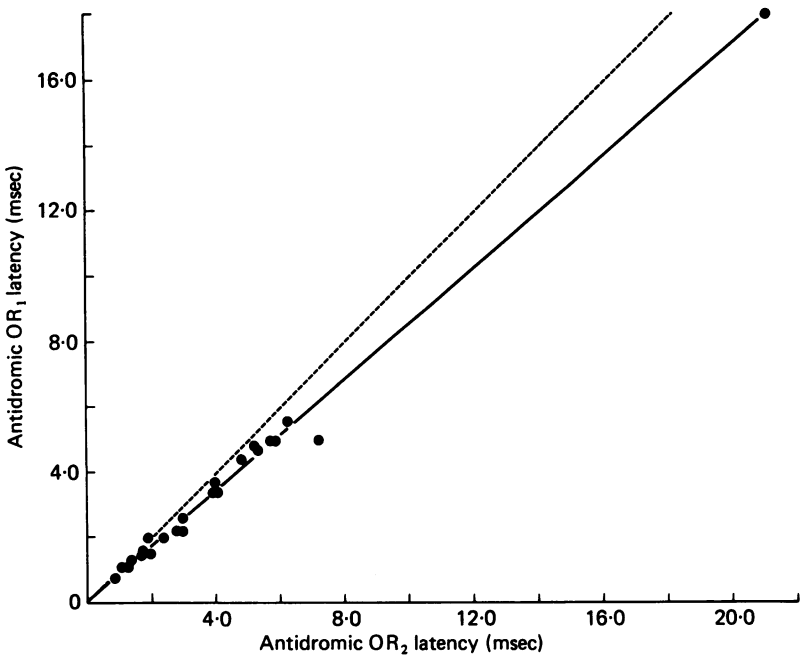

Fig. 6. Antidromic latencies of corticothalamic neurones activated from both pairs of OR stimulating electrodes. OR_1, posterior pair; OR_2, anterior pair. Dashed line, expected latencies if both pairs are in the same position; continuous line, regression line through experimental points.

in Fig. 6, 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 (cf. Tsumoto *et al.* 1978).

Laminar distribution of corticotectal and corticothalamic neurones

For a comprehensive analysis of corticofugal pathways it is important to know the lamina of origin of antidromically activated neurones. Many subcortically projecting cells were marked with electrolytic lesions, some examples of which are shown in Pl. 1. The histological location of the seventy-nine cells antidromically activated from the superior colliculus and/or optic radiation is summarised in Fig. 7. In this Figure, the positions of all corticofugal units are shown in a schematic representation of the left lateral gyrus. The majority of corticotectal cells are encountered 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.

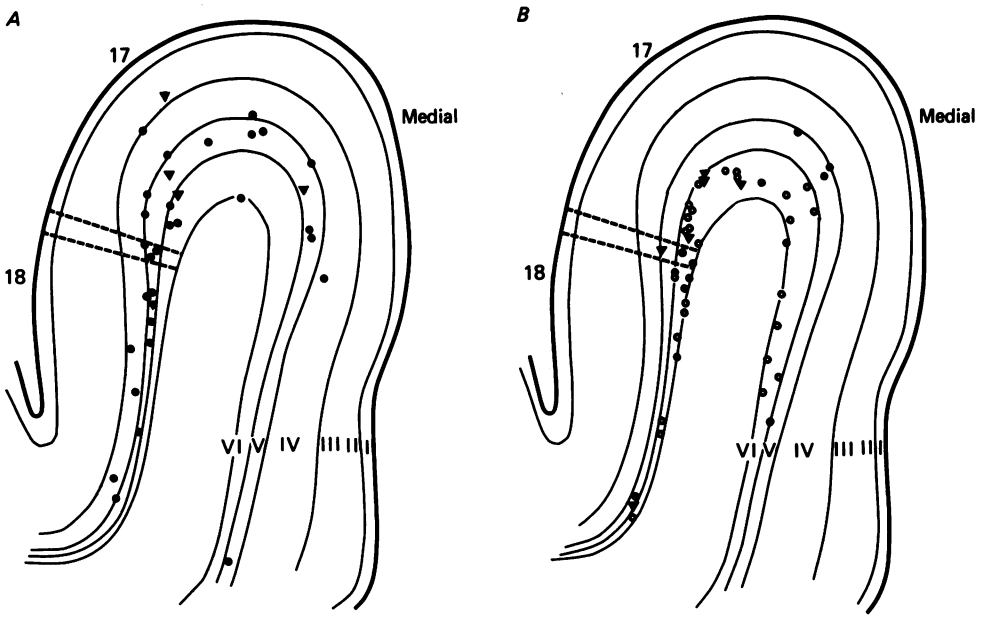

Fig. 7. Schematic representation of the left lateral gyrus showing the laminar disposition of corticofugal cells. *A*: corticotectal units; *B*: corticothalamic units. Area within dotted lines represents 17–18 border zone. Filled circles, C and C_H cells; open circles, S cells; filled triangles, unclassified cells.

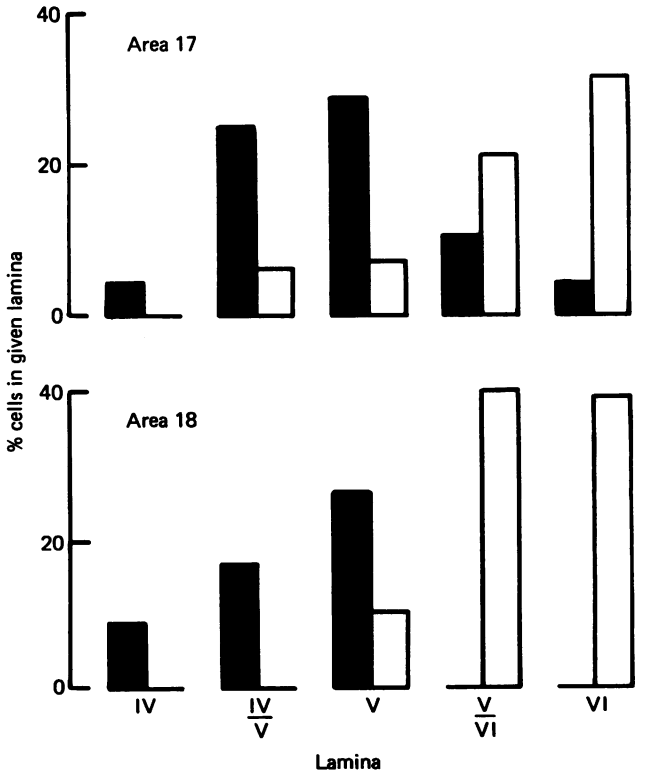

Fig. 8. Proportions of units in each of the deeper cortical laminae with axons efferent to the superior colliculus (filled blocks) or thalamus (open blocks). Units encountered at the boundaries between laminae have been placed in separate border groups (Henry *et al.* 1979; cf. Harvey, 1980).

In total, 283 cells were recorded between laminae IV and VI; 178 in area 17, 13 in the 17–18 border zone, and 92 in area 18. For each lamina in area 17 and area 18, the proportion of corticocollicular and corticothalamic neurones has been calculated and expressed as a percentage of the total number of cells encountered in that layer (Fig. 8). There is clearly a marked similarity in the over-all distributions between area 17 and area 18. In both cases, corticotectal cells comprise about 25% of the total number of cells recorded in layer V while about 30–40% of lamina VI cells have efferent axons.

The relative proportions of efferent S and C cells

It is of interest to know how many cells in a given receptive field class give rise to corticofugal axons. Fig. 9 shows the relative proportions of cells in the S and C families, encountered in the deeper laminae, which sent axons to the superior colliculus or to the thalamus. The data are pooled from both the striate and parastriate cortex, since the pattern in the two areas is almost identical. Fifty per cent 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 S.C. and OR electrodes. Corticothalamic S cells are found exclusively below lamina V. Of the total number of S cells encountered in layer VI, 45% sent axons out of the cortex.

Cells not responsive to visual stimuli

A number of cells encountered in laminae IV–VI in area 17 and area 18 could not be placed in any of the receptive field groups. These cells have been put into two categories: those that are very difficult to activate with visual stimuli and those that are responsive but cannot be satisfactorily ascribed to one particular receptive field class. As described above, about 70% of C cells in laminae V and VI and 45% of S cells in lamina VI give rise to efferent fibres. By contrast, of the forty-two apparently unresponsive cells recorded in these layers (including the IV–V border) only nine (19%) were antidromically activated from the S.C. and/or OR electrodes, and of these just two were orthodromically excited from the chiasm or radiation. The correlation between visually and electrically unresponsive cells in area 18 has been discussed elsewhere (Harvey, 1980), and the observation that only a few visually non-drivable cells have efferent axons raises the possibility that many may be interneurones.

The afferent input to corticotectal and corticothalamic neurones

Of the seventy-nine neurones antidromically activated from the optic radiation and/or superior colliculus, thirty-eight were also *orthodromically* driven from the OR and/or OX stimulating electrodes. Eighty-three per cent of efferent cells in parastriate cortex were orthodromically activated compared with 30% of corticofugal striate neurones. The higher proportion of orthodromically excited cells in area 18

is presumably related to the fact that area 18, unlike area 17, receives predominantly fast conducting thalamic afferents (cf. Harvey, 1980). The orthodromic OR latencies of S cells in area 17 ranged from 1·6 to 2·2 msec. One of these efferent cells was also driven from the optic chiasm and the OX and OR latencies for this cell were 3·5 and 1·7 msec, respectively, which suggests a relatively slow, direct input to this neurone. The OR latencies of striate C cells, on the other hand, ranged from 2·5 to 5·0 msec.

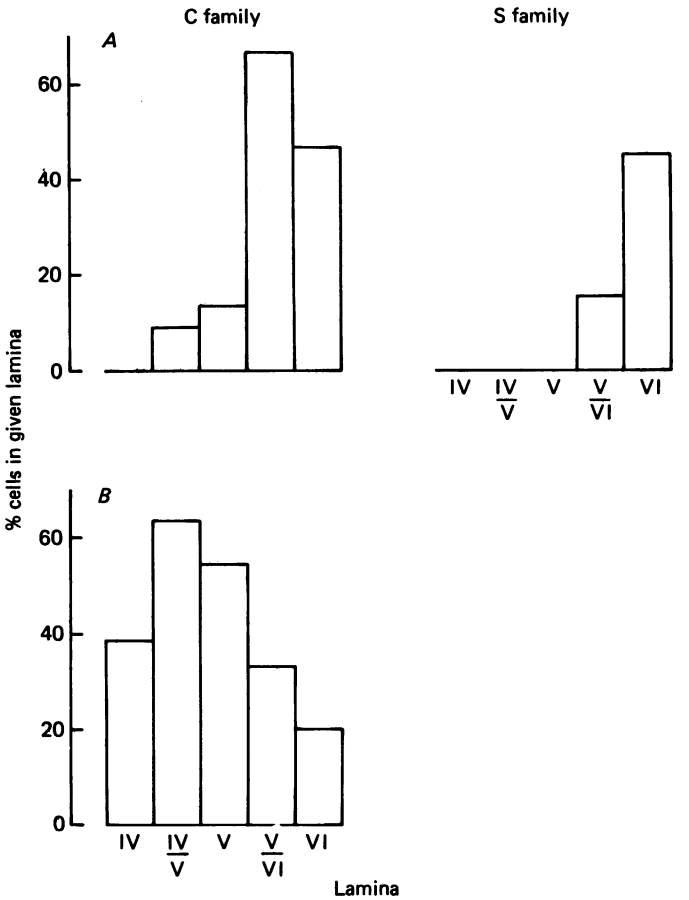

Fig. 9. Relative proportions of cells in the S and C families in each lamina which send axons to the thalamus (*A*) or superior colliculus (*B*). Data pooled from areas 17 and 18.

Two of these neurones (one corticocollicular and one corticothalamic) each had OX and OR latencies of 3·5 and 2·5 msec, respectively, which is suggestive of an indirect input by fast afferent fibres (Harvey, 1980). In area 18, all orthodromically excited efferent S cells had OR latencies less than 2·0 msec (1·1–1·8 msec) while corticofugal C cells had latencies ranging from 2·0 to 4·0 msec. Four of the S cells and nine of the C cells were also driven from the optic chiasm at latencies ranging from 2·3 to 2·9 msec and 3·1 to 5·0 msec, respectively. The OX–OR latency differences for all these cells are indicative of innervation by rapidly conducting afferents. In the previous paper (Harvey, 1980), parastriate neurones were divided into two main groups on the basis

of their orthodromic OX and OR latencies. It was argued that group 1 and group 2 cells are monosynaptically and disynaptically excited, respectively. Efferent S cells in area 18 belong exclusively to group 1 while corticothalamic and corticocollicular C cells generally have group 2 latencies. From the above it is apparent that although S cells have more slowly conducting efferent axons, they are none the less orthodromically excited at shorter latencies than corticofugal C cells. Furthermore, the present results provide no support for the proposal that corticotectal cells are monosynaptically driven by Y afferents from the d.l.g.n. (Hoffmann, 1973). Many corticocollicular neurones (especially those in area 18) are indirectly excited by fast conducting afferent fibres; however, the lack of OX activation of many efferent C cells in area 17 suggests that these particular cells may be innervated by more slowly conducting axons.

Part 2

Commissural projections

Electrical stimulation of the commissural system was tested on 417 units recorded in areas 17 and 18. Fifteen (4%) were activated antidromically and ninety-five (23%) orthodromically after stimulation of the corpus callosum and/or contralateral cortex. Two cells were activated both antidromically and orthodromically after callosal stimulation. For the antidromically driven cells, the latencies to callosal stimulation ranged, with one exception (8·1 msec), from 0·8 to 2·5 msec. The mean is 1·8 msec. Most orthodromically excited cells have c.c. latencies less than 3·0 msec. Four efferent cells and twenty-nine orthodromically activated cells were excited from both the corpus callosum and contralateral visual cortex; hence the conduction velocity of the commissural fibres involved in these projections can be calculated. Estimating the conduction distance between the recording electrode and the c.c. and c.v. stimulating electrodes to be approximately 17·5 and 31·0 mm respectively, the mean conduction velocity of callosal axons is about 13 m/sec with a range from 1·4 to 27·0 m/sec. Nearly two thirds of the axons have conduction velocities between 9 and 17 m/sec.

Receptive field properties of commissurally activated neurones

A wide variety of receptive field classes were antidromically activated after commissural stimulation. In area 17, one S, two S_H and one A cell were antidromically driven while in area 18, three S cells, one C_H and one B cell were found to project through the callosum. Within the 17–18 border zone itself, one S_H, one C and two A cells were antidromically activated. The anatomical location of the other two antidromically driven cells was not determined. One was classed as an S_H cell, the other was apparently unresponsive to visual stimulation. All types of cells could also be orthodromically excited by commissural stimulation. However, cells in the complex family (both the C and B groups) were excited more often than other cell classes. About 50% of all C and B type cells recorded in these experiments appear to receive callosal afferents.

The ocular dominance distribution (Hubel & Wiesel, 1962) of antidromically driven cells is shown in Fig. 10*A*. The distribution of orthodromically excited cells is

shown for comparison but it should be noted that ocular dominance could not be satisfactorily determined for all of these cells. Efferent commissural cells have either monocular or binocular receptive fields. The six monocularly driven cells were classed as A (three), S (two) and S_H (one), while the C, C_H and B cells were all in ocular dominance groups 3 and 4. The majority (80 %) of orthodromically excited cells for which ocular dominance could be determined have binocular receptive fields.

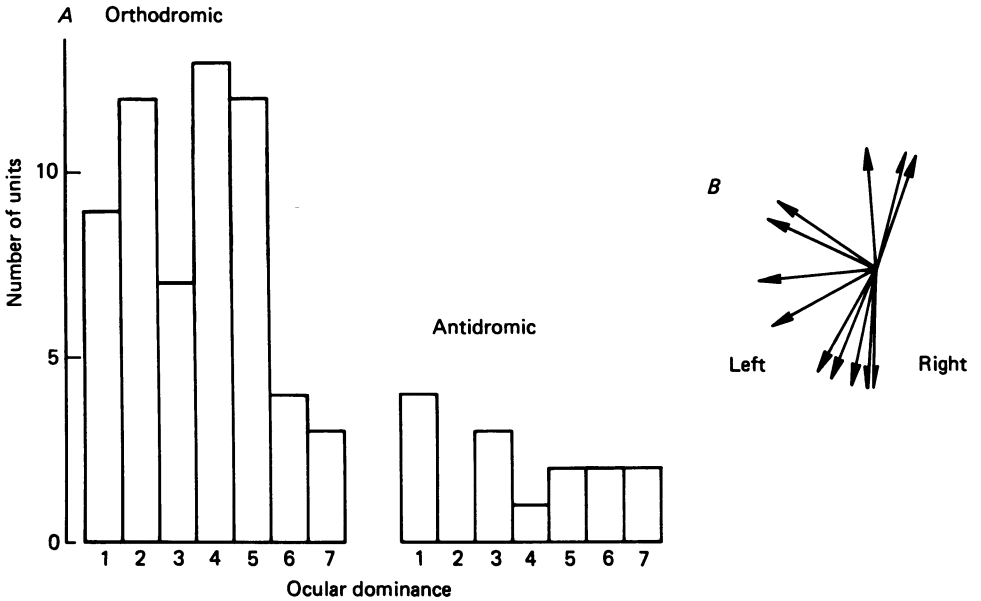

Fig. 10. *A*, ocular dominance distribution of cells antidromically or orthodromically activated after commissural stimulation. Ocular dominance expressed on a scale ranging from 1 (driven solely from contralateral eye) to 7 (driven solely from ipsilateral eye) (cf. Hubel & Wiesel, 1962). *B*, optimal direction of visual stimulus movement for antidromically excited cells. Left, ipsilateral visual field; right, contralateral visual field.

Twelve of the antidromically activated cells showed a clear preference for stimulus movement in one direction. The optimal direction of movement for each of these units is shown in Fig. 10 *B*. All efferent neurones 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.

The relationship between commissurally driven neurones and the 17–18 border

Anatomical studies have shown that the commissural projections into and out of the striate and parastriate cortex are densest at the border between the two areas (Hubel & Wiesel, 1965; Garey *et al.* 1968; Wilson, 1968; Heath & Jones, 1970, 1972; Shoumura, 1974; Innocenti & Fiore, 1976; Shatz, 1977). The location with respect to the 17–18 border was histologically determined for 313 of the units tested by commissural stimulation; 107 were in area 17, 34 were located within the 17–18 border zone and 172 were found in area 18. Thirteen of the localised cells were antidromically

activated and sixty-nine orthodromically activated. The highest proportion of efferent cells was found within the 17–18 border zone. Nearly 12% of all units recorded in this region were antidromically activated from the commissural electrodes.

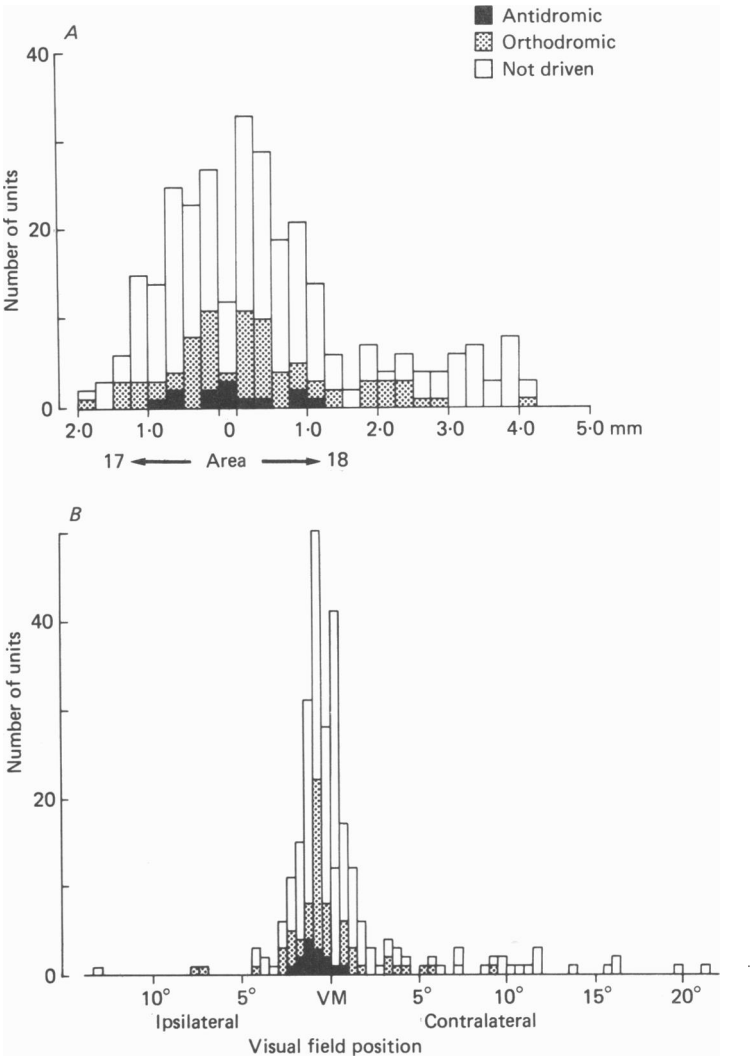

Fig. 11. Histological location (*A*) and visual field position (*B*) of cells tested by electrical stimulation of the corpus callosum (c.c.) and contralateral visual cortex (c.v.). *A*: position with respect to the 17–18 border; *B*: position with respect to the vertical mid line (VM). Filled blocks, antidromically activated cells; stippled blocks, orthodromically activated cells; open blocks, cells not excited from c.c. or c.v.

Fig. 11*A* presents a detailed analysis of the histological location of antidromically or orthodromically driven units. 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 stippled 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 are found within 1 mm either side of the 17–18 border. Cells orthodromically activated from the callosum are more widespread in their distribution, and are commonly found up to 3 mm into area 18.

The visual field position of cells activated by commissural stimulation

In Fig. 11 *B* the data have 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 have receptive field centres close to the vertical mid line; however, some orthodromically activated cells have fields up to 9° into the *contralateral* and up to 8° into the *ipsilateral* visual field.

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. 1). An exact statement concerning the extent of the ipsilateral visual field representation in the visual cortex is not possible due to the difficulty in defining the area centralis and the orientation of the vertical mid line in the paralysed cat. 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 each other out since the data in Fig. 11 *B* contains visual fields from both the ipsilateral and contralateral eyes. Given the possible errors (up to perhaps 2°) in relating the position of a cell's visual field with the vertical mid line, there are still some cells with receptive fields which appear to be in the ipsilateral visual hemifield. Although the majority of these units are only 1 to 1·5° from the vertical mid line (cf. Nikara, Bishop & Pettigrew, 1968; Leicester, 1968; Blakemore, 1969; Tusa, Palmer & Rosenquist, 1978), some have receptive fields much further out, the most distant being about 13° in the ipsilateral hemifield. Nearly all of these peripherally located cells were driven only by the contralateral eye. Interestingly, some of the cells with receptive fields in the ipsilateral hemifield were orthodromically excited after electrical stimulation of the optic chiasm and ipsilateral optic radiation. Their OX and OR latencies were always suggestive of activation by fast conducting afferent fibres (cf. Harvey, 1980).

The laminar distribution of commissurally activated neurones

The laminar distribution of cells antidromically or orthodromically activated after commissural stimulation is shown in Fig. 12. The proportions of antidromically or orthodromically excited cells in each layer are expressed as a percentage of the total number of cells tested by commissural stimulation in each layer. Data are pooled from areas 17 and 18 and the 17–18 border zone. Efferent callosal cells in both area 17 and area 18 are predominantly located in lamina III, and are found most often in deep III near the III–IV border. This result is in agreement with the anatomical studies of Innocenti & Fiore (1976) and Shatz (1977). By contrast, orthodromically activated cells were encountered throughout all cortical layers and the highest percentage of these cells occurs in laminae II, III and the IV–V border region. The distribution of orthodromically excited cells has the same basic form in both the striate and parastriate cortex.

Integration of primary and commissural pathways

In some experiments, electrodes were placed in the optic chiasm and ipsilateral optic radiation. In area 18, three efferent callosal cells were excited from both sites and had OX and OR latencies of 1·3–1·6 msec, and 2·4–2·8 msec, respectively. These latencies are suggestive of a direct input from fast conducting primary afferent fibres

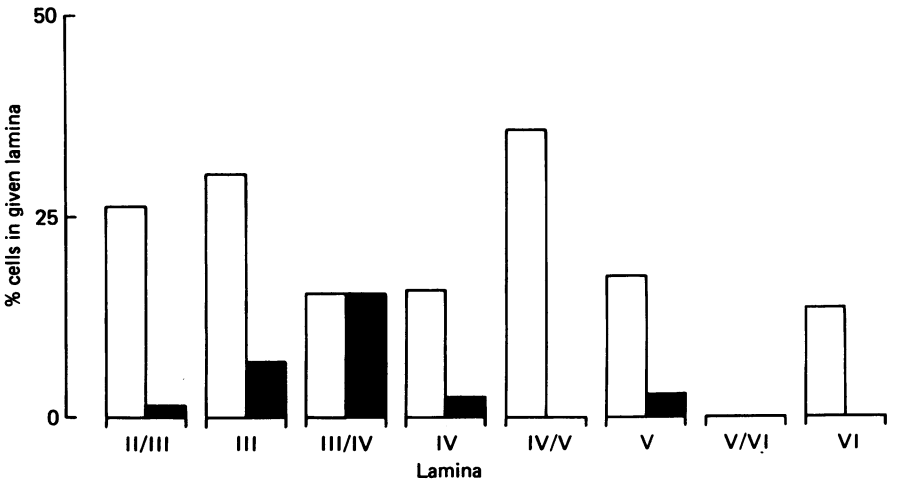

Fig. 12. Proportion of cells in each cortical lamina antidromically (filled blocks) or orthodromically (open blocks) activated after electrical stimulation of the corpus callosum and/or contralateral visual cortex. Data pooled from areas 17, 17–18 and 18. Cells encountered at the boundaries between laminae have been placed in separate border groups.

(Harvey, 1980). Most parastriate cells activated orthodromically after commissural stimulation had OX and OR latencies in the order of 3·2–4·0 msec, and 2·2–3·0 msec, respectively. The orthodromic latencies of these cells are typical of group 2 neurones as defined elsewhere (Harvey, 1980) and suggest that cells which apparently receive callosal fibres are generally driven indirectly by fast fibres from the ipsilateral d.l.g.n. (cf. Singer *et al.* 1975; Tretter *et al.* 1975). Interestingly, some cells with monocular receptive fields were orthodromically excited from both the primary and callosal pathways, which suggests that commissural input does not necessarily give rise to overt binocularity in cortical cells.

DISCUSSION

Corticotectal projections

HRP studies indicate that corticotectal neurones are restricted to lamina V of both the striate and parastriate cortex (Hollander, 1974; Gilbert & Kelly, 1975; Magalhães-Castro *et al.* 1975; Baleydier, 1977). Consistent with this observation, the majority of antidromically activated corticotectal cells are located at the IV–V border and in lamina V. However, occasional corticocollicular units are encountered

in more superficial and deeper layers (Fig. 8), which suggests that on a number of occasions the micro-electrode records from parts of the neurone distal to the cell body. The anatomical studies show that the large pyramids in layer V are always labelled after a collicular injection. Further, the short antidromic latencies of corticotectal neurones suggest that their axons and presumably their cell bodies are large. Since the smaller, long latency corticothalamic cells are never encountered outside layer VI, it would appear that recording at a site away from the soma only occurs when the larger cells in the cortex are involved. It is not clear whether the electrode is recording from the apical dendrites or axons of these cells. 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. Similarly, the number of C cells in layer V itself is likely to be higher than previous estimates have indicated (cf. Harvey, 1980).

The role of the corticotectal pathway in visually guided behaviour has not been clearly resolved. In general terms, the superior colliculus appears to be involved in certain aspects of visual attention and perception and in the control of head and eye movements during behaviours such as foveation and visual following (e.g. Sprague & Meikle, 1965; Norton, 1974; Roucoux & Crommelinck, 1976). At the single unit level, many cells in the cat superior colliculus receive convergent excitatory inputs from retinotopically related regions in areas 17, 18 and 19 (McIlwain, 1977), and inactivation of visual cortex results in a loss of binocularity and direction selectivity in tectal neurones (Wickelgren & Sterling, 1969; Rizzolati *et al.* 1970; Rosenquist & Palmer, 1971; Mize & Murphy, 1976). None the less, removal of areas 17 and 18 does not apparently alter the visuomotor behaviour of cats (Sprague, Levy, DiBerardino & Berlucchi, 1977).

The present results indicate that neurones in areas 17 and 18 efferent to the tectum are C cells. In general, corticotectal cells have large receptive fields, are broadly tuned for stimulus orientation and are responsive to a wide range of stimulus velocities. Thus whatever the exact role of the corticotectal system, the information transmitted from visual cortex is more related to the movement and general location of a visual stimulus than to fine details about the shape and position of the object. The fact that the axons of corticotectal cells are invariably fast conducting is consistent with the view that this system is concerned with dynamic rather than static visual behaviour. It is worth noting however, that although the Clare–Bishop cortex seems to be involved in visual transformations similar to those mediated by the tectum (Baumann & Spear, 1977; Kennedy & Magnin, 1977; Sprague *et al.* 1977), it does not receive an input from striate C cells but is instead innervated mostly by B cells (Henry *et al.* 1978; cf. Henry *et al.* 1979).

Corticothalamic projections

A major problem with the technique of electrical stimulation is the difficulty in determining exactly what pathways are being stimulated. Since almost all corticotectal fibres are also activated from the optic radiation, care must be taken to distinguish between stimulation of axon terminals and fibres of passage. The analysis so far has assumed that cells activated from the OR but not from the tectum are projecting to the thalamus. Consistent with this, the majority of cells excited only

from the OR are located in lamina VI, the origin of the corticogeniculate pathway (Gilbert & Kelly, 1975; Tombol *et al.* 1975).

It seems likely that striate and parastriate S cells project onto neurones within the d.l.g.n. All efferent S cells are located in layers V–VI and VI and are commonly excited from the anterior OR electrodes placed near or more usually just within the d.l.g.n. Further, axons of efferent S cells are slowly conducting and therefore of small diameter, which is consistent with anatomical evidence that the corticogeniculate projection contains many fine fibres (Guillery, 1967; Niimi, Kawamura & Ishimaru, 1971; Kawamura, Sprague & Niimi, 1974). In addition, as described previously (Harvey, 1978*a*), there is a close correlation between the antidromic latencies of efferent S cells, on the one hand, and the orthodromic latencies of intrageniculate interneurones obtained after electrical stimulation of the visual cortex (Cleland, Levick, Morstyn & Wagner, 1976; Dubin & Cleland, 1977) on the other.

Interneurones located within the d.l.g.n. are believed to play an important role in the precise, retinotopically organized inhibitory pathways found within this nucleus (e.g. Dubin & Cleland, 1977; Singer, 1977). Corticofugal S cells, especially in area 17, are very specific in their stimulus requirements and there would be a great deal of redundancy if such cells projected onto a diffuse inhibitory network. Rather, they are more likely to be involved in the specific pathways mediated in part by intrageniculate interneurones. Of particular relevance in this context is the suggestion of Schmielau & Singer (1977) and Singer (1977) that the corticogeniculate projection is concerned with the control of binocular interactions in the d.l.g.n. (cf. Harvey, 1978*a*). Their proposal requires 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 d.l.g.n. by suppressing binocular inhibition in the corresponding projection column as well as by facilitating the cells within this column. Cells for which binocular images are non-optimal would be inhibited (Barlow, Blakemore & Pettigrew, 1967; Pettigrew, Nikara & Bishop, 1968; Bishop, Henry & Smith, 1971) and intrinsic inhibitory interactions within these projection columns would predominate. As a result, the signals from binocularly viewed objects near the fixation plane are selectively facilitated while those from objects away from the fixation plane remain suppressed by inhibitory interactions within the d.l.g.n. If the visual cortex is to play such a role, the cells feeding back to the geniculate must themselves be highly sensitive to the relative positions of binocularly viewed stimuli. S cells are finely tuned to binocular spatial disparity (cf. Nelson, Kato & 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 d.l.g.n.

Tsumoto *et al.* (1978) have used cross-correlation analysis and iontophoretic application of glutamate to examine the corticogeniculate system. Their results seem to indicate that large field binocular complex cells provide the input to lateral geniculate neurones. However, most of the corticogeniculate latencies derived from their cross-correlograms were between 2 and 7 msec which is compatible with the antidromic latencies of S rather than C cells (Fig. 5). Further, and perhaps more importantly, the cross-correlation observed by Tsumoto *et al.* (1978) requires that there is a spatial correspondence between the cortical and geniculate neurone. The

apparent lack of efferent S cells may therefore be due to the difficulty in finding such pairs when small and highly specific receptive fields are involved and where *exact* superimposition of these fields is necessary.

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 d.l.g.n. cells. It is possible that effects would be more noticeable in intrageniculate interneurones rather than relay cells. Since interneurones are recorded only rarely (e.g. Dubin & 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 & Singer (1977), for example, used spots of light, a stimulus which is by no means optimal for corticothalamic S cells in area 17 (see Results). Therefore, even with an intact cortex, the corticogeniculate system will not be exerting its maximum effect.

A number of large field, binocular C cells in lamina VI were activated antidromically from the optic radiation but not from the tectum (cf. Tsumoto *et al.* 1978). These cells have fast conducting axons and their latencies appear to be too short to account for the input to intrageniculate interneurones, unless one postulates the existence of complicated polysynaptic circuits or suggests that recruitment of a number of fast conducting fibres is necessary to produce a suprathreshold excitatory post-synaptic response (cf. Harvey, 1978*a*). Such a diffuse innervation by large field C cells seem unlikely given the nature of the inhibitory pathways within the d.l.g.n. As suggested elsewhere (Harvey, 1978*a*), it is possible that these lamina VI C cells are innervating cells in the perigeniculate nucleus. A projection onto this nucleus from both areas 17 and 18 has been described anatomically (Kawamura *et al.* 1974; Updyke, 1975, 1977) and the visual properties of efferent C cells seem appropriate for participation in the diffuse, non-specific inhibitory pathways mediated by perigeniculate neurones (Dubin & Cleland, 1977; Singer, 1977). The small number of corticofugal C cells in laminae IV–V and V which do not project to the tectum may be projecting to thalamic regions other than the d.l.g.n. and the perigeniculate nucleus. It is possible, for example, that they are efferent to the pulvinar complex (Lund *et al.* 1979). 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 d.l.g.n. is so sparse. It may be that many lamina V corticocollicular cells branch and send axon collaterals to these thalamic regions (cf. Guillery, 1967; Lund *et al.* 1979). These same layer V cells may also project to the pons (Gibson, Baker, Mower, Robinson & Glickstein, 1978*b*).

Commissural projections

Unlike other corticofugal pathways, where a given projection arises from cells with similar visual properties, the receptive fields of efferent callosal cells form a remarkably heterogeneous group. This diversity is presumably related to the fact that a number of visual functions are mediated by the interhemispheric pathways. These appear to include mid line stereopsis (Mitchell & Blakemore, 1970), the control of ocular vergence movements (Westheimer & Mitchell, 1969; Blakemore, 1970) and the unification of the two visual hemifields (Choudhury, Whitteridge & Wilson, 1965).

However, despite this heterogeneity, some specific details about the visual callosal projection do emerge from the present physiological analysis and these are briefly considered below.

In binocular vision, a population of visual cortical neurones with differing receptive field disparities is thought to provide the neurophysiological substrate for binocular depth discrimination (Barlow *et al.* 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 retinae respectively. If it is assumed that temporal retina projects only ipsilaterally and nasal retina only contralaterally, the two monocular images will project to opposite cerebral hemispheres. Binocularity in cortical cells coding for mid line stereopsis can arise only if units in the two hemispheres are subsequently interrelated by fibres passing through the corpus callosum. Evidence for the involvement of commissural pathways in mid line stereopsis has been obtained in man (Blakemore, 1970; Mitchell & Blakemore, 1970) as well as in cat and monkey (Choudhury *et al.* 1965; Vesbaesya, Whitteridge & Wilson, 1967; Berlucchi & Rizzolatti, 1968). However, in both monkey and cat, a vertical strip of retina does exist which contains both ipsilaterally and contralaterally projecting ganglion cells, and a given cerebral hemisphere can therefore receive fibres directly from either both nasal or both temporal retinae, independent of the callosum (Stone, Leicester & Sherman, 1973; Stone & Fukuda, 1974; Kirk, Levick & Cleland, 1976; Kirk, Levick, Cleland & Wässle, 1976; Bunt, Minckler & Johanson, 1977).

Bishop & Henry (1971) have proposed that there are two kinds of stereopsis. Fine stereopsis requires closely matched binocular images and operates over a narrow range of spatial disparities. The overlap of crossed-uncrossed X or brisk sustained cells observed in the retina may well be sufficient to allow binocular cortical neurones to code for mid line stereopsis independent of interhemispheric pathways. Certainly, cortical cells with receptive fields in the ipsilateral visual hemifield are commonly encountered at the 17–18 border (cf. Fig. 11 *B*), and Leicester (1968) has shown that this representation is still present after section of the corpus callosum. Coarse stereopsis on the other hand, which is much less specific in that it does not require similar visual stimuli in the two eyes and can operate up to spatial disparities of 7 or 8°, is suggested as requiring transcallosal connexions. Bishop & Henry (1971) regard the stimulus disparities used by Blakemore (1970) and Mitchell & Blakemore (1970) as being suitable for testing the presence or absence of coarse, but not fine, stereopsis. The present study has shown that although efferent callosal cells have receptive fields close to the mid line, some units apparently receiving commissural fibres have receptive fields up to 9° in the contralateral and up to 8° 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°. This possible range of spatial disparities is very similar to the behavioural limit of 7 or 8° required by coarse stereopsis. Although very large receptive field disparities were only infrequently encountered, it may be that the input from the contralateral hemisphere is relatively

weak and not recognized using qualitative methods which involve monocular testing of each eye in turn. It should also be noted that the delay of 3–5 msec or more which results from projection through the callosum may be additionally important if the perception of depth depends upon temporal as well as spatial factors (Cynader, Gardner & Douglas, 1979).

Callosal connexions may also play a role in the visual tracking of objects moving from one hemifield to the other (cf. Dow & Dubner, 1971). It might be expected, therefore, that the stimuli of particular relevance in this situation would generally be those moving towards the vertical boundary between the two hemifields, since only those stimuli would be about to cross from one visual hemifield to the other. Efferent callosal cells tend to have preferred directions of movement towards the ipsilateral visual field (Fig. 10) and may therefore be alerting the contralateral hemisphere to the fact that an object is about to enter its visual hemifield.

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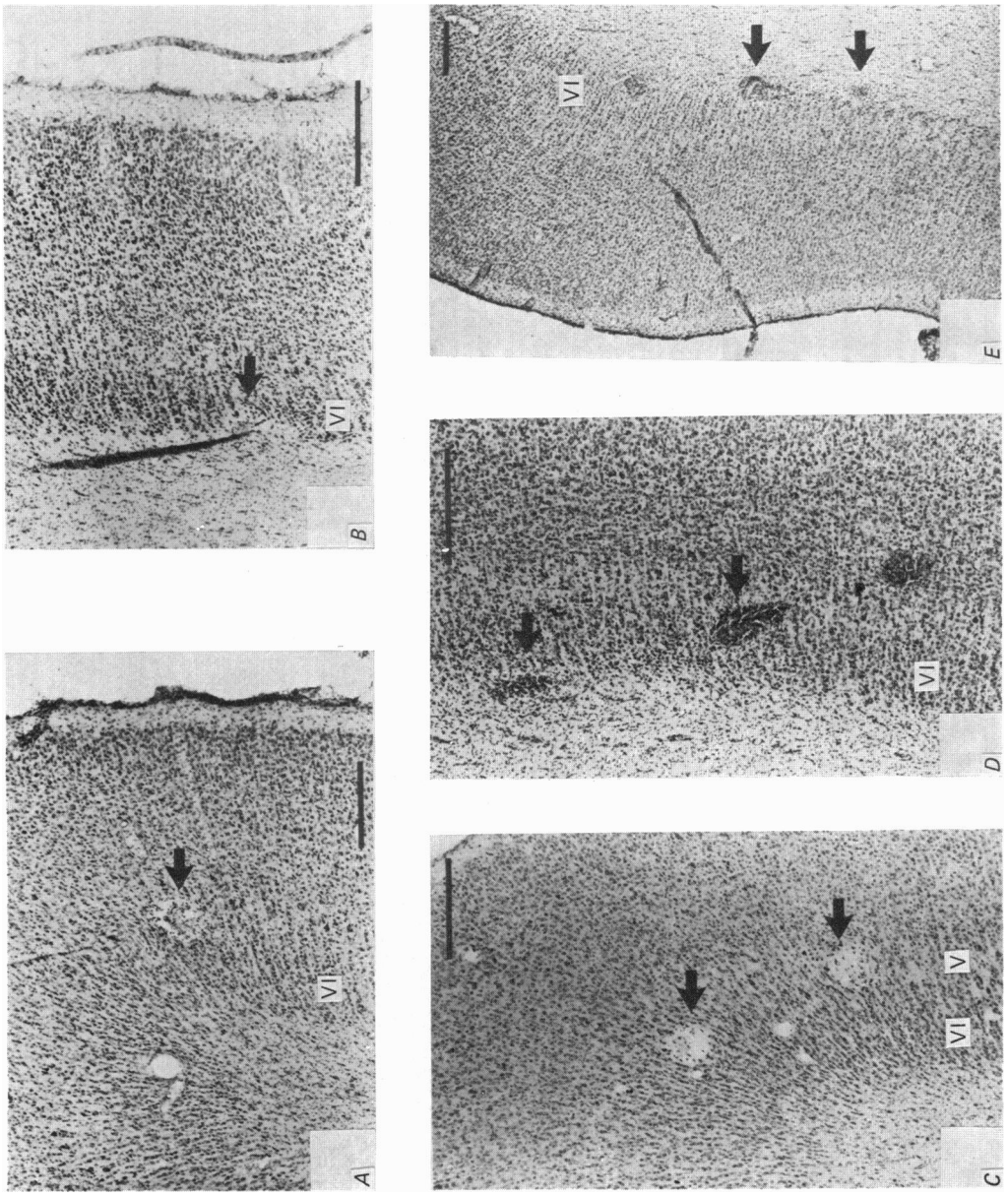
EXPLANATION OF PLATES

PLATE 1

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 position of cortico-thalamic neurones with the exception of the bottom lesion in *C* which shows the location of a corticocollicular unit. *A–D*, penetrations in the medial bank (area 17). *E*, penetration in the lateral bank (mostly area 18). *A–E*, scale markers, 500 μm.

PLATE 2

Photomicrograph of a Nissl-stained section showing 17–18 border zone. Dashed lines indicate limits of border region. Arrows show the position of large pyramidal cells located deep in lamina III. Scale marker, 500 μm.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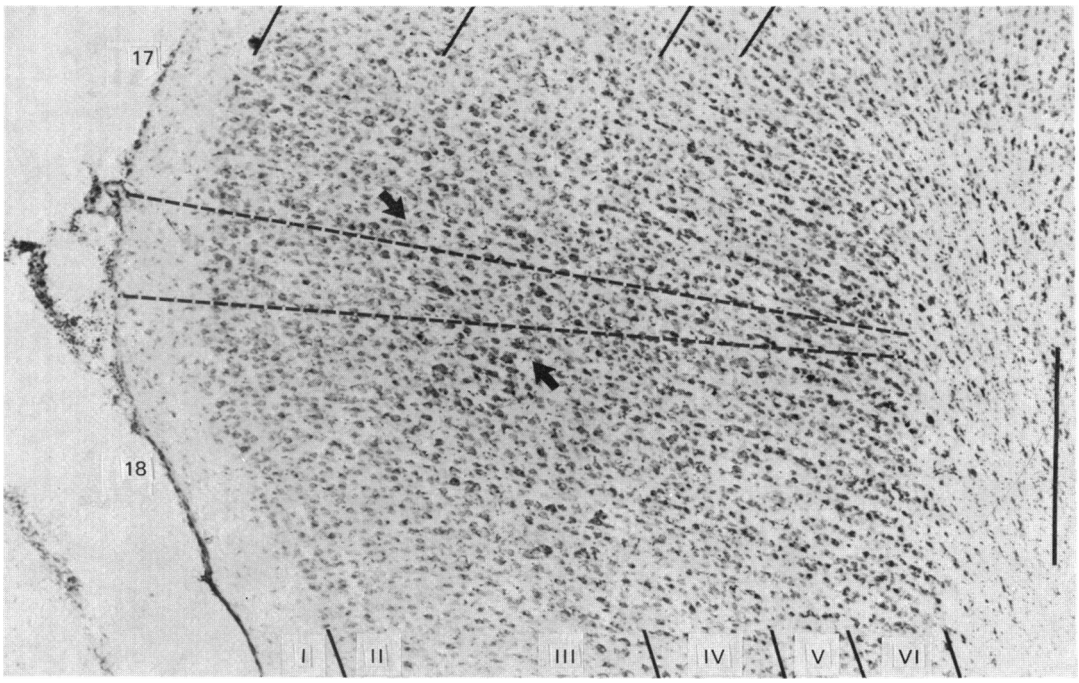
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