STUDIES ON THE CONNECTIONS OF THE VISUAL SYSTEM

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" STUDIES ON THE CONNECTIONS OF THE VISUAL SYSTEM "

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ABSTRACT OF THESIS

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Title of Thesis STUDIES ON THE CONNECTIONS OF THE VISUAL SYSTEM

The visual responses have been studied, by recording with tungsten micro-electrodes, in the nucleus interlaminalis medialis, the superior colliculus, the cerebellar visual area of the cat, and the superior colliculus of the baboon.

A. THE NUCLEUS INTERLAMINALIS MEDIALIS OF THE L.G.N.

1. The secondary retinal representation has been determined on the cat's L.G.N., and the observation of Seneviratne and Whitteridge (1962) that the upper visual field is represented in the posterior part of the nucleus has been confirmed. In addition, the representation of the lower field has also been found in the anterior part of the nucleus. Some degree of retinotopic organization on the N.I.M. has been shown.

2. Twelve single units were observed and these had either 'on' or 'off' center with receptive fields larger than in the main nucleus.

B. THE SUPERIOR COLLICULUS OF THE CAT

1. The retinotopic organization has been described on the surface of the superior colliculus which has been flattened out and the ratio 1.5:1 of the surface areas between the lower and the upper field quadrants was obtained. There is a close correlation between the magnification factor and a centro-peripheral retinal ganglion cell density (Stone, 1965) along the horizontal meridian.

2. 150 units have been classified into 5 groups according to the size of the receptive fields and the optimum responses to moving stimuli (small receptive field unit, medium receptive field unit, large receptive field unit, directionally selective unit, and specific orientation unit). The majority of units responded only to movement and required different velocities as their optimum stimuli. In general, the velocity increased as the receptive field increased in size. The functional significance of units in the superior colliculus concerned with eye movement control has been discussed.

3. The influence of the visual cortex upon single units in the superior colliculus has been studied by cooling the corresponding parts of the visual cortex and the visual responses of 7 units were found to be abolished.

C. THE BABOON'S SUPERIOR COLLICULUS

1. The retinotopic projection on the surface of the superior colliculus, which has been flattened out, has been mapped. In general, the pattern of projection is similar to that in the cat, but there is no disparity between the areas of the superior colliculus devoted to the upper and lower visual field quadrants. There is evidence of macular representation on the anterior pole of the superior colliculus. The magnification factor along a horizontal meridian has been measured and a close correlation with a centro-peripheral retinal ganglion cell density was obtained.

P.T.O.

Use other side if necessary.

2. Eight single units, which were similar in behaviour to those in the cat, have been observed. Apart from the non - directional units, two specific orientation units have been found.

D. THE CEREBELLAR VISUAL AREA OF THE CAT

1. The visual responses in the cerebellum have been studied by moving stimuli, and the extent of the visual responsive area is confined to the Declive (lobule VI) and Folium-Tuber vermis (lobule VII).

2. The visual responses of 104 units, which were classified into 4 groups according to the behaviour of the units in responding to moving stimuli, have also been studied. Most of the units responded to movements, usually of fast speed, and showed habituation to repeated stimuli. One type of directionally selective unit, "the centrifugal unit ", showed a preferential response to movement in a centrifugal direction (moving away from the center of fixation). The possible role of the units in the cerebellar visual area in the mechanism of eye movements has been discussed.

SUMMARY

The visual responses have been studied, by recording with tungsten micro-electrodes, in the nucleus interlaminalis medialis, the superior colliculus, the cerebellar visual area of the cat, and the superior colliculus of the baboon.

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INTRODUCTION

I. THE OPTIC NERVE, CHIASM AND OPTIC TRACT

A. ANATOMICAL ASPECTS

In the cat, the optic nerve is composed chiefly and perhaps exclusively of the axons of retinal ganglion cells, presumably in a 1:1 relationship as suggested by Arey and Gore (1942) for the dog. Nevertheless, the possibility of centrifugal fibers passing from the brain through the optic nerve cannot be excluded by either these studies or those reported by Bishop (1953), who counted 127,000 optic nerve fibers and 125,000 retinal ganglion cells in the cat. According to Stone (1965) the total number of ganglion cells in the retina is approximately 90,000. Other reported counts of the cat's optic nerve are within the same range, considering experimental error; 119,000 (Breusch and Arey, 1942); 120,000 (Bishop et al, 1953). Apparently, all optic nerve fibers in the cat are myelinated, and Bishop and Clare (1955) have found a size range from 0.5-12.0 u with the majority in the 1.0 u range; although, using the electronmicroscope, they have noted myelinated fibers as fine as 0.2 u. Electrophysiological work by Hubel and Wiesel (1962) has suggested that some unmyelinated fibers may be present. Bishop and Clare (1955) have also suggested a rather even distribution throughout the nerve of fibers of different size but were unable histologically to confirm the four fiber groups described in their electrophysiological studies. On the other hand, Chang (1952) and Lennox (1958), using electrophysiological techniques, have independently reported three chief fiber groups in the cat optic nerve; whereas anatomical studies by Bishop et al (1953) have described two principal fiber groupings at 1.0-1.5 u and 4.0-4.5 u with over 80% of all fibers having a diameter of less than 3 u.

The optic chiasm is a complex interchange of optic nerve fibers with fibers from the nasal portions of each retina decussating into the contralateral optic tract, the most anterior of these decussating fiber bundles detouring slightly into the contralateral optic nerve (Polyak, 1957). Fibers from the temporal third of each retina, lateral to the meridian through the area centralis, do not cross at the optic chiasm but enter the ipsilateral optic tract. No precise count of the number of crossed and uncrossed optic tract fibers in the cat has been reported, but Polyak (1957) estimates that about 50-70% of these fibers cross. Walls (1942), Doty (1958), and Hayhow (1958) estimate that about two-thirds cross.

B. CONDUCTION VELOCITY

In classifying the conduction velocity of fiber groups in the cat optic tract, Bishop and O'Leary (1938), applying a shock to the optic nerve of the cat, found the volley of impulses splitting into an early large and a later somewhat smaller wave with average conduction velocity of 30-40 m./sec.

with the wave front at 70 m./sec.. Bishop et al (1953) recorded monophasic antidromic action potentials at a point 6 mm. from the crushed end of the optic nerve following stimulation of either the contralateral or ipsilateral optic tract. Conduction velocities in this experiment were 30-40 m./sec. (mean 34) for the fastest, 17-23 m./sec. (mean 21) for the intermediate, and 15-20 m./sec. (mean 18) for the slowest fibers.

Chang (1952) reported somewhat different values for the conduction velocities of fiber groups in the cat optic nerve: 70, 30, and 17 m./sec. for the fastest, intermediate, and slowest groups respectively. In the same study it was also reported that three peaks of distribution lying in the region of 1, 4, and 9 u of the fiber caliber spectrum. Chang (1956) in confirmation of his earlier work, found that the three peaks of antidromic action potentials could be recorded when both ipsilateral and contralateral optic tracts were stimulated simultaneously.

The measurements by Lennox (1958) on 73 single fibers, using glass microelectrodes with tip diameter of 0.15-0.4 u, calculated for the mean measured distance between stimulating and recording electrodes (41 mm.), the three significant latency groups corresponding to conduction velocities of about 52, 37 and 16 m./sec.. Clearly this technique fails with small fibers below 2 u, which are the majority.

Bishop and Clare (1955) could not confirm Chang's observation. They concluded from the electrophysiological data that the fibers of the optic nerve show four groups which differ in conduction velocity. The most rapidly conducting fibers (8-12 u diameter, and conduction velocity 40-50 m./sec.), carry information to the visual cortex with a synapse in layer A of the dorsal nucleus of the lateral geniculate nucleus; the next fastest fibers, 4-8 u diameter and conduction velocity 15-25 m./sec., travel to layer B of the same nucleus and then to the lateral nucleus of the thalamus; the third fastest group innervates the pretectal area, and the slowest fibers go to the superior colliculus. The ratios of conduction rates of groups are roughly 2:1 for successive pairs, the ratios of threshold are greater than 1:2.

So far, there is disagreement, as to whether there are two (Bishop et al, 1953), three (Chang, 1952; Lennox, 1958) or four (Bishop and Clare, 1955) groups with different conduction velocities and fiber diameters or whether the distribution curve according to fiber diameter is smooth.

From available data (Bishop and Clare, 1955) one would be forced to conclude that the small fibers do not project to the cortex. But Granit and Marg (1958), by stimulating in the tract and recording from the ganglion cells of the rabbit's retina with microcapillaries, found that many of the optic nerves come from the smaller ganglion cells which belong to cones; and in the cat, by antidromic stimulation, the largest and fastest fibers have been shown to come from the giant ganglion cells (Granit, 1955). The good correlation between conduction velocity and the size of ganglion cell spike supports the contention that fiber size actually is related to the size of ganglion cell (Maturana, 1959).

II. THE LATERAL GENICULATE NUCLEUS

A. HISTOLOGICAL STUDIES OF THE LATERAL GENICULATE NUCLEUS

The morphological characteristics of the cat's lateral geniculate nucleus have received a great deal of attention.

The lateral geniculate nucleus consists of three discrete elements:-

1. The pars dorsalis
2. The pars ventralis
3. The nuclei perigeniculatus, anterior and posterior.

THE PARS DORSALIS

In parasagittal section, the pars dorsalis is a convoluted cellular mass of S shape consisting of an almost vertical plate of cells, with its long axis lying in the transverse plane. The bulb of the pars dorsalis consists of the basal limb of the S, a relatively thick plate of cells, almost semi-spheroidal in shape, lying in the horizontal plane at right angles to, and becoming continuous with, the posterior and dorsal plate of cells. Thuma (1928) has described 3 principal cellular laminae of the pars dorsalis which he designated A, A1, and B, dorsal to ventral, separated from one another by two sparsely cellular, interlaminar fiber plexuses. Barris (1935) has discerned in it four layers in agreement with that described in the dog by Rioch

(1929). The various descriptions, however, are essentially equivalent and differ only in terms of discreteness accorded to the layer of large cells present between the two ventral laminae A1 and B. These two laminae have each a characteristic cellular structure and are separated from each other, not by a prominent medullary lamina, comparable with that of the more dorsally placed A-A1 interlaminar plexuses, but rather by a cellular transitional zone characterised by the presence of scattered, large, deeply staining cells. These large cells were considered by Thuma, the "nucleus interlaminalis centralis". Rioch, in Nissal stained sections of the dog's lateral geniculate nucleus, described a discrete lamina magnocellularis lying immediately ventral to the A1 lamina. Barris (1935), using Rioch's terminology, described the lamina magnocellularis in the cat as a thick and irregular layer of large cells present in the thickened anterior segment of the pars dorsalis, being completely absent in the posterior segment where the laminae are aligned one behind the other.

THE PARS DORSALIS

The two dorsal laminae A and A1 are of identical histological structure and are separated byA A1 interlamina fiber plexus. Anteriorly, where the laminae are horizontally disposed, they are 20-25 cells thick, but posteriorly, where the laminae are vertical each is greatly reduced in thickness, being here less than 10 cells thick. These two cellular laminae are characterized by a fairly uniform distribution of small (10-20 u), medium (20-25 u) and large (30-40 u) cells, in number generally inversely proportional to their size. Hayhow (1958, 1959), confirms the views of Tello (1904), Cajal (1955), Tabaada (1927), O'Leary (1940), and Bishop (1953), who have described the cells in the pars dorsalis as belonging to two main types, principal and short axon cells respectively. The principal cells are those whose axons enter the optic radiation, while the short axon cells have processes confined to their laminae of origin. The cells tend to be aggregated into small clusters or glomeruli containing six to eight cells, their dendrites, arising from several shafts, branch extensively at their origin to give rise to an exceedingly dense protoplasmic plexus. The dendrites of cells whose bodies are situated away from the surface of a layer arborize in all directions, the cells situated near the surface of a layer having most of their dendrites directed towards the center of the layer. O'Leary (1940) found the short axon cells scattered throughout the three laminae, but in all cases the distribution of the axons and dendrites was limited to the layer in which the cell body was situated.

THE PARS DORSALIS B

Pars dorsalis B is also a sigmoid lamina containing medium size spindle-shaped cells, situated between pars dorsalis A1 dorsally and the layer of dispersing optic tract fibers ventrally. It is of greatest thickness in the center of the anterior pole of the pars dorsalis where the laminae are horizontal, being reduced in extent in the posterior vertical segment and almost absent in the extreme lateral and anterior aspects of the pars dorsalis. Cajal, O'Leary and Hayhow have drawn attention to the histological features of this lamina which distinguished it from the A and A1 laminae; its characteristic population of spindle cells, its afferent supply by predominantly small diameter fibers, and the orientation of the terminal axon arborization in the plane of the lamina and not radially across it as they are in the A and A1 laminae. Hayhow (1958) has suggested the existence of a functional differentiation for lamina B from these differences.

NUCLEUS INTERLAMINALIS MEDIALIS

Thuma (1928) also described a diffuse cluster of cells situated between the pars dorsalis laterally and the pulvinar medially; dorsally and ventrally this defined plate of cells was limited by the rami of the optic tract, this group of small cells being named "nucleus interlaminalis medialis". A similar intermingling of cells in the posterior region of the pars dorsalis with those of the pulvinar has been described in the dog by Rioch.

Hayhow (1958), in a comprehensive study, has made it possible to clarify the nature of the rather obscure most medial region of the pars dorsalis, which Thuma has designated as the nucleus interlaminalis medialis. He described the nucleus interlaminalis medialis as three poorly defined, approximately vertically orientated bars of cells, which from medial to lateral, are continuous with pars dorsalis B, the ventral component of pars dorsalis A1 and pars dorsalis A and B. These groups of cells are situated along the medial edge and just under the medial edge of the main nucleus. On account of the general similarity in the distribution of the homolateral and contralateral optic tract fibers within the pars dorsalis and the region of the nucleus interlaminalis medialis, it is justifiable to view the latter as a relatively independent accessory pars dorsalis.

THE PARS VENTRALIS

The pars ventralis is a small pyramidal mass of cells located between the medial and lateral rami of the optic trat, ventrolateral to the pars dorsalis and separated from the latter by a thin fiber stratum. It is composed predominantly of very small cells (5-10 u). Anteriorly it becomes continuous with the nucleus perigeniculatus anterior.

THE NUCLEI PERIGENICULATUS, ANTERIOR AND POSTERIOR

The nucleus perigeniculatus anterior is an attenuated, irregular layer of small cells, forming a cap over the anterior and dorsal surface of the pars dorsalis A. The nucleus perigeniculatus posterior forms a cap of small cells over the posterior end of the pars dorsalis A1 and is in apparent continuity with pars dorsalis B.

B. ELECTROPHYSIOLOGICAL STUDIES OF THE LATERAL GENICULATE NUCLEUS

The major electrophysiological method in studying the lateral geniculate nucleus is the study of "evoked potentials", elicited by electrical shocks, or light, and considerable amount of this work has served two main purposes: either to further understanding of the general problems of synaptic transmission in the central nervous system, and to elucidate the nature of the sensory input of the visual pathways, The studies of synaptic transmission in the lateral geniculate nucleus are reviewed by Crescitelli (1960), and Bishop (1964). This latter author concentrated on certain aspects of the properties of the geniculate neurons such as interpretation of unit wave forms, spontaneous activity, repetitive firing and refractory period of geniculate neurons.

Largely through the work of Kuffler (1953, 1957) in the cat, and Barlow (1953 a,b) in the frog, retinal ganglion cells are known to have a well defined, concentric receptive field arrangement. Hubel (1960), by recording from single units in the unrestrained cat with tungsten microelectrodes, studied the patterns of firing and responses to diffuse and restricted light stimuli, and found that most geniculate cells responded briskly to diffuse light stimuli. In sleep, the units tended to fire impulses in brief, high frequency clusters. Arousal or activation by light stimulation abolished these clusters.

Similar firing patterns and responses were recorded from fibers in the optic radiation and the striate cortex below layer IV. These fibers were presumed to be geniculate axons. These had a concentric arrangement of excitatory and inhibitory ('on' and 'off') regions, similar to that described for retinal ganglion cells by Kuffler (1953).

Hubel and Wiesel (1961), studied the single unit responses in the lateral geniculate nucleus of the cat under sodium pentothal anaesthesia and immobolised the eyes by succinylcholine. They stimulated the retina with a spot of light subtending 2° at the eye and with the annulus of light subtending 2°-6° at the eye between its inner and outer borders. They found that, in their general arrangement, geniculate receptive fields resembled those retinal ganglion cells described by Kuffler (1953) and Wiesel (1960), having an excitatory ('on') center and inhibitory ('off') periphery, or the reverse. The two portions of a receptive field were mutually antagonistic. Cells recorded in layer A and B of the lateral geniculate nucleus were driven from the contralateral eye; cells in layer A1 from the ipsilateral eye. All these layers contained both 'on' center and 'off' center units. Cells in layers A and A1 were similar both in their firing patterns and in average receptive field size. Cells in layer B were more sluggish in their responses to light stimuli, and tended to have a larger receptive field center.

Seneviratne and Whitteridge (1962), and Seneviratne

(1963) have also recorded activity in single units in the cat's geniculate nucleus, anaesthetised with chloraloe, and have excited the units by a small spot of light subtending 1/2-2°. Of 162 units studied, they found that the upper surface of both layers A and A1 contain "center on" units and the loer surface of both contain "center off" units. All B units are extremely sensitive to stray light, and react strongly to changes in background illumination, in contrast to the more sluggish responses of layer B by Hubel and Wiesel (1961), under barbiturate aneasthesia. Other barbiturates, including nembutal, also suppress the responses (Whitteridge, unpublished observations).

The activity of the cells in lamina B seems different to those of A and A1 in many aspects: by virtue of the absence of segregation of 'on' and 'off' center units, the greater proportion of 'off' units to 'on' units, the greater proportion of continuous 'off' with respect to short 'off' effects, and the greater proportion of units with larger receptive fields and lower thresholds. Some units in B had very low thresholds, almost equal to that of the fully dark adapted eye of the observers to the level of background illumination (Seneviratne, 1963).

Kosak et al (1965), studying the response of single units in the lateral geniculate nucleus of the cat to moving stimuli, using moving cardboard figures under servo-mechanism control, found the on-center units firing transiently either to the movement of a white figure into their receptive fields or the removal of a black figure. Conversely off-center units were found to fire transiently either to the movement of a black figure into, or a white figure out of, their receptive fields. The response patterns of L.G.N. units were found to vary in a characteristic manner as the size, shape and speed of the figure were varied.

C. PROJECTIONS OF THE RETINA TO THE LATERAL GENICULATE NUCLEUS

THE PARS DORSALIS

In the cat, the primary thalamic termination of optic fibers is the pars dorsalis of the lateral geniculate nucleus. From transneuronal studies, Minkowski (1920), Barris (1935), Silva (1956); from Nauta studies , Hayhow (1958); and from electrophysiological studies, Cohn (1956); it has been established that crossed optic fibers terminate exclusively in laminae A and B whereas uncrossed optic fibers terminate in the lamina A1 of each lateral geniculate nucleus.

Bishop and Clare (1955), studying the conduction velocity of the cat's optic tract, have shown that the fastest conducting group activates principally layer A (and A1 homolaterally) in agreement with the largest fiber observed by Cajal (1955); Thuma (1928); Barris, Ingram and Ranson (1935); O'Leary (1940); Bishop and O'Leary (1940). The next fastest group relays through layer B to the lateral nucleus of thalamus.

O'Leary (1940) has shown that individual optic tract fibers end within a single cellular layer and in the adjacent interlaminar margin. Individual lamina cells probably make synaptic contact with several different fibers. Each optic tract fiber of the cat probably terminates with extensive overlap in an area containing about 10 laminar or principal cells, Glees (1941), as opposed to the situation in the monkey where there is apparently little or no overlap of terminals of different fibers, Glees and Clark (1941). This overlap may provide in the cat a neuroanatomical basis for great sensitivity in low illumination.

Brindley (1960) suggested that the determination of the relationship between number of optic tract fibers and neurons within the L.G.N. could have important functional implications concerning possible modifications to transmitted visual information at thalamic level.

THE REPRESENTATION OF THE RETINA ON THE LATERAL GENICULATE NUCLEUS

Marchi degeneration studies reported by Overbosch (1927) indicate a retinotopic organization of optic terminals within the pars dorsalis of the lateral geniculate nucleus, with the lower retinal quadrants represented dorsal to the upper and the temporal quadrants represented lateral to the nasal. Since Overbosch (1927) no further anatomical studies have been carried out in respect to the retinotopic projections in the cat. Additional information is available from studies of retrograde geniculate degeneration following cortical lesions, Minkowski (1913), Putnam and Putnam (1926), and Polyak (1927).

Seneviratne and Whitteridge (1962), and Daniel et al (1961) have also studied the topographic representation of the visual field on the lateral geniculate nucleus in the cat. They claim that the retinal mapping agrees well with the other data, and the central 9°-10° occupy almost half of the nucleus, but the field below the horizontal meridian seems to have an exaggerated representation. In addition, they have also found the second representation of the retina at the medial tip of the nucleus which is the mirror image of the first nucleus and has about 1/4 of the magnification factor. They have not found behavioural differences between the twoareas. They explained that the second visual area is apparently identical with the nucleus interlaminalis medialis.

Bishop et al (1962), studied the projection of the retina on the L.G.N. of the cat, using a system of polar-co-ordinates, with polar axis passing through the nodal point of the eye, at right angles to the presumed fixation plane. They found the upper field quadrant projecting posteriorly on the nucleus with the lower field anteriorly and the peripheral field lateral on the nucleus.

Seneviratne (1963) gives the information in detail, that the central part of the right visual hemifield is projected on the medial aspect of the left nucleus, the lower field quadrants on its dorsal and antero-inferior aspects, while the upper field quadrant is presented on the surface of the postero-medial curl which represents only the upper field quadrant. At that time the lower field quadrant had not yet been found.

The existence of a secondary area at geniculate level has also been observed by Chouhury and Whitteridge (1964) in the rabbit. Though the responses from their secondary area apparently do not conform to a mirror image of the whole of the primary area, here a reduplication of the lower nasal field of primary area is indisputable.

The disparity of areas devoted to the upper and lower field quadrants of L.G.N. of the cat do not, however, seem to have these differences reflected in the ganglion cell counts of upper and lower retina, Seneviratne (1963). These cell counts seem to fall off equally in both directions along the vertical plane passing through the area centralis, and similar findings are also obtained by Stone (1965) in making the quantitative analysis of distribution of the ganglion cells from the whole amount of the retina. The map shows a great increase in density at the central area and also in a horizontally orientated arm of relative high density extending from the central area into nasal and temporal retinae, but shows no difference between the upper and lower halves.

Recently, Laties and Sprague (1965), using Nauta-Laidlaw technique, confirmed Hayhow's studies, and they, after making lesions by photocoagulation, found that the nasal retina projected to four areas of the contralateral L.G.N.: laminae A and B, nucleus interlaminalis centralis, and medial part of nucleus interlaminalis medialis.

Temporal lesions projected ipsilaterally to three areas: Laminae A1, nucleus interlaminalis centralis, and lateral part of the nucleus interlaminalis medialis. Peripheral lesions yield medial focal areas of degeneration in the appropriate laminae. Central lesions give a greater degree of degeneration than peripheral lesions of comparable size. Focal degeneration is found in the nucleus interlaminalis medialis after either central or peripheral retinal lesions.

THE PARS VENTRALIS

O'Leary (1940) described terminations within the pars ventralis of collaterals from thin optic tract axons, which made synapses in the pars dorsalis. Hayhow (1958) has demonstrated termination of both crossed and uncrossed optic fibers within this nucleus, confirming earlier studies by Ramon Cajal (1904), Minkowski (1920), O'Leary (1940) and polyak (1957). Although Barris et al (1935) and Barris (1935) failed to demonstrate optic termination within the pars ventralis. Altman and Carpenter (1961), however, have shown that this nucleus receives afferent input through ascending fibers from the superior colliculus, and Altman (1962) has also described afferents to this nucleus from the pars dorsalis.

III. THE SUPERIOR COLLICULUS

CATS

A. HISTOLOGICAL STUDIES OF THE SUPERIOR COLLICULUS

Like other regions in the nervous system, the mammalian optic tectum has been subdivided differently by various observers, depending upon the animal studied and the particular relations the worker was seeking to emphasize. A nine layer pattern described by Tsai (1925) and Huber and Crosby (1943) is used as a basis for description of the cat's superior colliculus.

From above downward, these are:-

I. Stratum Zonale

This corresponds to the stratum zonale of Ramon Cajal (1955) and Winkler and Potter (1911, 1914) for the rabbit and the cat. It consists of a narrow band of fibers with small intercalated neurons.

II. Stratum griseum superficiale

This stratum is comparable to the stratum griseum superficiale of Winkler and Potter (1911, 1914) for the rabbit and the cat. This layer has small and medium-sized cells intercalated in course of outspread terminal fibers.

III. Stratum opticum

This layer corresponds to the stratum opticum of Ranson (1940) for man, and Tsai (1925) for the opossum.

It is well developed, shows some intercalated neurons, corticotectal and optic components with medullated fibers.

IV. Stratum griseum intermediale

This corresponds to the stratum griseum intermedium of Winkler and Potter (1911, 1914) for the rabbit and the cat, stratum griseum medium (Tsai, 1925) for the opossum. Relatively wide gray band, small to medium-sized cells intermingled with fiber fascicles, occasional larger neurons are the characteristics of this layer.

V. Stratum album intermediale

This is represented in the stratum medullare intermedium of Winkler and Potter)(1911, 1914) for the rabbit and the cat, stratum album medius of Tsai (1925) for the opossum. It is well developed, poorly delimited, with numerous fascicles, some intercalated cells.

VI. Stratum griseum profundum

This stratum appears to correspond to the stratum griseum profundum of Winkler and Potter (1911, 1914) for the rabbit and the cat, and Tsai (1925) for the opossum. It is not sharply delimited. Medium-sized triangular to pyramidal cells and occasional larger multipolar, relatively numerous fiber fascicles are the characteristics of this layer.

VII. Stratum album profundum

This is the homologue of stratum medullare profundum of Winkler and Potter (1911, 1914) for the rabbit and the cat, stratum album profundum of Tsai (1925) for the opossum. It has a distinct band of commissural and efferent fibers.

VIII & IX Stratum griseum et stratum fibrosum periventiculare

Most students of mammalian brains have not considered the periventricular layers as a part of the optic tectum. Often they have been included in the central gray. They are composed of small to medium-sized neurons with massing of the fibers internally, thinly medullated and unmedullated fibers, and cells of the mesencephalic root of V at outer border at many levels.

B. ELECTROPHYSIOLOGICAL STUDIES OF THE SUPERIOR COLLICULUS

A pioneer study was made on evoked potentials in the superior colliculus by Wang (1934), stimulating the retina with light, and by Wang and Lu (1936), stimulating by shadow movements across the visual field. Later, electrophysiological studies of the superior colliculus have been much devoted to the mechanism of the oculomotor system. Bishop and O'Leary (1941, 1942) analysed the potentials recorded from the superior colliculus of the cat and rabbit.

In lightly anaesthetised cats with sodium pentobarbital, Apter (1946) applied strychnine to a localized (1 mm^2) area of the right superior colliculus. If the light were then shone into the eyes, both eyes moved to fixate a single point in the left visual field irrespective of the eye position at the beginning of the movement. Each point on the superior colliculus was found to regulate movements of the eyes to a particular part of the visual field, medial points causing upward lateral movements, lateral points causing downward lateral movements, each colliculus always causing movements to the contralateral visual field. The map of fixated position on the surface of the superior colliculus more or less coincided with the electrophysiological map of the visual field on the superior colliculus.

Altman and Malis (1962), anaesthetised the cat with nembutal, recorded potentials from the superior colliculus and visual cortex evoked by light flashes at the eye and electrical stimulation of the optic nerve. Three functionally differentiated layers of the superior colliculus were distinguished; a dorsal layer in which evoked potentials and single units responding to optic stimuli were obtained; an intermediate layer in which evoked potentials of unchanged amplitude, but no driven units, were recorded; and a ventral layer in which evoked potentials were greatly reduced, and where only "spontaneously" discharging units were found. They classified the optically driven units as those firing with short latency, with long latency, to light-on only, to light-on and light-off, and those inhibited by photic or optic nerve stimuli. They interpret their three functional layers in terms of a dorsal layer of discharging cells which respond to optic stimulation, an intermediate layer of fibers which bring optic stimuli to the colliculus, and a ventral layer which contains cells that respond to extra-optic stimulation of unknown origin. The absence of histological control with the technique in this study leads them to comment that for definitive results on laminar organization, the microelectrode technique should be combined with histological identification of the exact sites of recording.

C. PROJECTIONS OF THE RETINA ON THE SUPERIOR COLLICULUS

Afferent connections of the superior colliculus of the cat enter chiefly through the stratum opticum or the stratum griseum intermediale, as observed by Cajal (1955) after enucleation of one eye, and Marchi degeneration was limited to the superficial fibers of stratum opticum. Huber and Crosby (1943) also claim that the retinotectal fibers pass dorsally, corticotectal fibers, ventrally. Cajal (1955) also demonstrated a rich and complex terminal arborization, especially for those optic fibers which terminate in the adjacent gray layers (stratum griseum superficiale and stratum griseum intermediale), but do not rise to the more superficial stratum zonale. This latter layer contains only corticotectal fibers which also ramify in the deeper layers. These have been confirmed by later workers - Polyak (1927), Mettler (1932), Barris et al (1935), Beresford (1961), and Altman (1962). Both anatomical data - Barris et al (1935), Altman (1962) - and physiological data - Apter (1945), Altman and Malis, (1962) - have shown many more optic fibers originating from the contralateral retina than from the ipsilateral terminate within the superior colliculus of the cat.

Bishop and Clare (1955) have demonstrated electrophysiologically that the third group of slow conducting fibers terminates in the superior colliculus and the latencies of the postsynaptic spike are 9-11 m/sec., giving an estimated conduction rate of approximately 3.5 m/sec.. This result is in agreement with the conduction rate 5 m/sec of retinotectal fibers, measured by Altman and Malis (1962).

Additional input to the superior colliculus includes ascending fibers from the brain stem and spinal cord through the spinotectal tract, and fibers from the reticular systems, all entering through the stratum album intermediale and ramifying in the adjacent gray layers (Huber and Crosby, 1943; Morin et al, 1951; and Anderson and Berry, 1959).

THE RETINAL REPRESENTATION ON THE SUPERIOR COLLICULUS

Studies of degenerating myelinated fibers following circumscribed lesions of the retina have shown the presence of a systematic projection of the retinal quadrants on the superior colliculus of the rabbit (Brouwer and Zeeman, 1923), rat (Lashley, 1934), but have failed for the cat (Brouwer and Zeeman, 1923). However, Hoessly (1947) demonstrated retinal quadrantic representation on the superior colliculus by means of the Marchi method, and the results establish differentiated representation of the peripheral fields on the optic tectum.

Apter (1945) has demonstrated electrophysiologically a systematic projection on the surface of the superior colliculus of the cat by recording action potentials with moist wick electrodes, using as a stimulus a spot of light subtending 4.2° in the field, finding the position of the electrode at which the evoked response was of minimal latency and minimal amplitude. She has found that there is a systematic projection of the temporal field or nasal retina of the left eye on the right superior colliculus, of the nasal field or temporal retina of the right eye on the left superior colliculus. The upper field is projected on the superior colliculus medial to the lower field. Points along the vertical meridian are projected at the anterior edge of the superior colliculus. In each collicular surface the representation of the ipsilateral temporal half field and the contralateral nasal half field were superimposed in such a manner that corresponding points in the homonymous half fields were in register.

MONKEYS

A. HISTOLOGICAL STUDIES OF THE SUPERIOR COLLICULUS

The superior colliculi of the primate greatly decrease in size and receive a decreasing number of optic fibers.

According to Huber and Crosby (1943) the following strata may be recognized:

I. Stratum Zonale

It is a narrow band of fibers containing a few small scattered neurons.

II. Stratum griseum Superficiale

It is composed of small to medium sized, frequently triangular neurons without regular arrangement.

III. Stratum Opticum

This layer is well developed but indistinctly delimited. Small intercalated neurons and medullated fibers are found.

IV. Stratum Griseum Intermediale

This stratum is fairly wide. Cells among fiber fascicles like those of stratum griseum superficiale are found.

V. Stratum Album Intermediale

This layer is composed of clusters of cells among fiber fascicles.

VI. Stratum Griseum Profundum

Small, medium and relatively large triangular, multipolar or polyhedral cells are found with numerous fiber fascicles.

VII. Stratum Album Profundum

This broad layer is composed of clear-cut medullated bundles; laterally are a few neurons of the overlying larger cells.

VIII & IX. Stratum Griseum at Stratum Fibrosum Periventriculare.

The cells are small, frequently spindle shaped neurons without regular arrangement and bordered internally by thinly medullated or un-medullated periventricular fibers.

B. PROJECTIONS OF THE RETINA TO THE SUPERIOR COLLICULUS

The projection of the retina is known to be in accordance with a definite pattern for various experimental animals. In the primates, the number of optic fibers to the superior colliculus is so greatly reduced that the attempts to obtain this pattern in the monkey have not been very successful, Crosby et al (1962).

Brouwer and Zeeman (1926) studied the projections of the retina in the optic center in the monkeys by Marchi method. They found the projection of the retina to the superior colliculus, but the fibers are very small, especially on the uncrossed side. They emphasized that the degenerations were constantly absent after macular lesions. They also suggested that in the monkeys there is a localization of the different parts of the retina in the superior colliculus but their material is, however, too limited to give a detailed scheme.

Daniel and Whitteridge have recorded the multiple responses from the superior colliculus of the monkey within 15^o-20^o of the visual axis and have pointed out that the peripheral field seems to have a very restricted representation, (Whitteridge, 1961).

IV. THE OCCIPITAL CORTEX

A. THE VISUAL AREAS

The occipital region of the cat has been studied by numerous investigators. Brodmann (1909), in his well known classification, has divided the occipital cortex of the cat into 3 areas: area striata (17), area occipitalis (18), and area preoccipitalis (19). Winkler and Potter (1914) suggested other names. Their preoccipital area is Brodmann's occipital area, and their paroccipital area is Brodmann's preoccipital area. According to Otsuka and Hassler (1962), based on Brodmann classification, the striate area occupies on the medial aspect - the splenial, suprasplenial, and postsplenial gyri; superiorly, a medial strip of the lateral gyrus and the postero-lateral gyrus. The occipital area (18) lies solely on the convexity in the middle of the lateral gyrus immediately lateral to the striate area, and extends to the bottom of the postero-lateral gyrus. The preoccipital area (19) surrounds both the others. It occupies the medial wall at the bottom of the splenial sulcus, and often also a part of the posterior suprasplenial gyrus.
Comparison with other authors; their occipital area is smaller than that of Winkler and Potter (1914), and Winkler and Potter (1914) show part of it on the medial aspect and in the splenial

sulcus, but Otsuka and Hassler do not find any there.

Recently Ebner and Myer (1965), using Nauta-Gyax silver technique, after total forebrain commissure transection in the cat, found that the striate cortex was remarkably free of degenerating fibers, while the part of area 18 lying lateral to area 17 on the lateral gyrus contains the greatest number of degenerating fibers. A narrow part lying just lateral to the area 18 on the convexity is free of interhemispheric connections.

The cytoarchitectonic and myelotectonic structure of the occipital region has been studied by Campbell (1905), Brodmann (1906), Winkler and Potter (1914), O'Leary (1941), and Otsuka and Hassler (1962) with some modifications. The six layers according to Brodmann are named, from above downward: I. Lamina molecularis, II. Lamina granularis externa, III. Lamina pyramidalis, IV. Lamina granularis interna, V. Lamina ganglionalis, and VI. Lamina multiformis. The area striata of the cat was also thoroughly investigated by Ramon Cajal (1922). At that time, he reduced his original nine to an eight layer plan, and indicated the corresponding levels of the Brodmann classification.

The structural plan of the area striata of the cat was studied in detail by O'Leary (1941), using Nissl and Golgi preparations, but he suggested other names. The names of the layers, corresponding to Brodmann, are as follows:
I. Plexiform, II. Modified superficial pyramids, III. Super-

ficial pyramids, IVa. Star pyramids and star cells, IVb. small star cells, Va. Pyramids with arciform axons, Vb. Large internal pyramids, and VI. Basal pyramids.

B. ELECTROPHYSIOLOGICAL STUDIES OF THE OCCIPITAL CORTEX

In the cat's visual system, the receptive field arrangement of single cells suggested that there is a greater degree of complexity than at the lower level of the visual system. Hubel (1960), Hubel and Wiesel (1959, 1962, 1963, 1965), in their extensive work in electrophysiology of the visual system, have shown that visual messages undergo considerable modification, within the retina, lateral geniculate nucleus, and especially visual cortex. Retinal ganglion cells respond optimally to an appropriately placed spot of light just the right size, a smaller or larger is less effective. Cells at these levels therefore register, not simply the illumination between a region and its surround. In the striate cortex cells are far more complex.

The cortical cells may be classified by function into three large groups (Hubel and Wiesel, 1959, 1962, 1965). The first group of "simple" cortical cells responds to line stimuli - such shapes as slit (light lines on a dark background), dark bars or edges. For maximal response the position and orientation of the receptive field axis vary from column to column. The second group of "complex" cells also responds best to line stimuli, provided that, as with simple cells, the shape is suitably orientated for the particular cell under observation. Complex cells, however, are not so discriminating as to the exact position of the stimulus, provided that it is properly orientated.

The third group of cells, 'hyper-complex', can be divided into 2 subgroups: lower-order hyper-complex cells, like complex ones, but the length of the stimulus had to be limited in one or both directions. This kind behaves as if it received inputs from two complex cells or sets of cells, one excitatory to the cell, with receptive field occupying the activating region, and one inhibitory to the cell, having its field in the antagonistic portion. The higher-order hyper-complex cells, however, differ from the lower-order hyper-complex in responding to the line in either of two orientations 90° apart, and the point where the terminations of the line or edge fall within the receptive field is necessarily critical. These cells behave as if they have their input from a large number of lower-order hyper-complex cells.

The great majority of cells in visual II and half of the cells in visual III are complex, lower-order hyper-complex cells. 5-10% of the cells in visual II, and about half of those in visual III are higher-order hyper-complex. (Hubel and Wiesel, 1965).

C. PROJECTIONS TO THE VISUAL CORTEX

The primary afferent supply to the striate area of the cat comprises the optic radiations from the lateral geniculate nucleus - Minkowski (1913), Polyak (1927), O'Leary (1941), and Sholl (1953, 1955) - which passes into Gennari's line, there to ramify extensively. Sholl (1955) concluded that each geniculate fiber may influence up to 5000 neurons within a volume of 0.1 mm^3 of cortex.

Electrophysiological evidence has shown that the caudal part of the middle suprasylvian gyrus obtains its principal supply from the pulvinar, and the rostral part of this gyrus from the lateral thalamic nucleus, Waller and Barris (1937), and the postero-medial extent of this gyrus from the lateral geniculate nucleus (Polyak, 1927).

Vastola (1961) obtained short latency responses at the medial lip of the middle part of the contralateral suprasylvian gyrus by stimulating the optic nerve electrically. The response in the suprasylvian cortex is not altered by isolating the ipsilateral gyri lateralis, postero-lateralis, splenialis, and suprasplenialis or by destroying the contralateral L.G.N. or optic tract. The response is abolished by anodal polarization of the ipsilateral L.G.N. These observations suggest that the suprasylvian area represents a direct pathway activated by fast fibers from the ipsilateral

L.G.N. and the striate cortex which receives the primary radiation fibers is part of a considerably larger cortical area innervated by a system of secondary fibers. In addition, the primary and secondary fibers originate in the geniculate cells innervated by the fastest group of fibers in the optic tract. Vastola suggests that the group of cells in the ventrolateral portion of the dorsal nucleus of the lateral geniculate body is the site of origin of the secondary response.

THE RETINAL REPRESENTATION OF THE OCCIPITAL CORTEX

Talbot (1940), Talbot and Marshall (1941), mapped electrophysiologically the retinal representation on the occipital cortex. By this method, the left half of each retina was found to project to the left cortex, the right half to the right; the lower field is forward on the brain, the upper occipital. The vertical meridian of vision extends forward and backward along the midline. The upper right quadrant of the field projects to the left gyrus compositus medialis, with the extreme right periphery around the lateral tip of sulcus lateralis. The lower right quadrant projects to the medial wall of the left marginal gyrus, with the periphery along the upper lip of sulcus splenialis. The right horizontal meridian follows the lateral limb of sulcus splenialis inward toward the midline.

Talbot (1942), also has described the second visual area as related anatomically to 18; it seems lateral to the line, diagonally along the lateral gyrus into the bottom of the postero-lateral sulcus; and confined anteriorly to the lateral gyrus and posteriorly to the suprasylvian.

Bilge, Seneviratne, and Whitteridge (1963) also mapped the visual cortex of the cat, and have confirmed the work of Talbot (1940) for visual I, that the largest part of this area lies on the medial surface of the cerebral cortex, at its posterior pole, and to a slight extent on the tentorial surface, only a strip a few millimeters wide is to be found on the dorsal surface. They have added the information that the lower field below the horizontal meridian has much greater representation than that above the horizontal meridian. Lateral to the visual I they have also observed Talbot's visual II, occupying the greater part of the lateral gyrus, as a mirror image representation of the lower half of the visual field.

Hubel and Wiesel (1965), using electrophysiological and histological methods, described the visual areas I, II, and III. They commented that these physiologically defined areas, visual I, II, and III, are identical to the areas defined anatomically as 17, 18 and 19. The boundary between 17, 18 and 19 can thus be assessed by four independent methods, the Nissl-stain, the myelin stain, silver degeneration technique, and physiological mapping. In their experiments so far, they have shown only the transitions between visual I, II and III on the dorsal surface of the visual cortex which represents only the lower field, but have neither information on the cortical area that adjoins 17 deep in the splenial sulcus and a region that Otsuka and Hassler designate as 19, nor on the posterior portions of 17, 18, and 19 where superior visual fields have their representation.

V. THE DESCENDING VISUAL PATHWAYS

A. CENTRIFUGAL FIBERS TO THE RETINA

There has been considerable anatomical evidence which indicates the existence of efferent fibers. Ramon y Cajal (1894), quoted by Granit (1962), described the fibers which terminate on the amacrine cells, and suggested that these fibers originated from somewhere outside the retina. Similar conclusions were drawn by Polyak (1957), and Maturana (1959).

Granit (1955) recording from the retinal ganglion cells, investigated the effects of stimulation of the temporal region of the reticular formation, and concluded that the potentiation and inhibition, initiated by stimulation in the tegmental part of the reticular formation or even by stimulation of the optic tract, is due to stimulation of the centrifugal fibers.

On the concept of centrifugal fibers to the retina, Granit (1962) also writes "..We now have the general picture that somewhere, perhaps within the tectum, efferent myelinated fibers possibly non-myelinated in mammals arise which end on amacrine cells or within the plexiform layers, but it would be of great value, in view of Ramon y Cajal's experiments with the dogs to be able to exclude recurrent collaterals".

Fillenz and Glees (1961) investigated the occurence of degeneration of the cat optic nerve fibers. Two different groups of fibers are distinguished which degenerated along two different time courses. One group consisted of fine fibers of 0.5-1.0 u in diameter and showed slower time course of degeneration. It is quite conceivable that these fibers are centrifugal fibers to the retina. (Motokawa, 1963).

Cowan and Powell (1962, 1963), making lesions in the midbrain, demonstrated neurohistologically the degenerating centrifugal fibers to the retina in the pigeon. These fibers are larger than the normal optic fibers. Brooke, Downer, and Powell (1965), using the same technique, show centrifugal fibers to the retina of the cat and monkey. After section of the optic nerve in the cat, changes are seen in a few fibers in the optic nerve of the retina. The affected axons, as in the pigeon, are larger than the optic nerve fibers. In the inner plexiform layer, occasional degenerating fibers and terminals are seen.

B. CENTRIFUGAL FIBERS TO THE LATERAL GENICULATE NUCLEUS

Barris, Ingram and Ranson (1935), reported degeneration after lateral gyrus lesions in the superior colliculus not in the lateral geniculate nucleus of the cat. Altman (1962) has reported projections from superior colliculus to the lateral geniculate nucleus (layers A, A1, and intervening interlaminar area) and the posterior nucleus of the thalamus. In the rat, Nauta and Bucher (1954) have reported corticofugal projections to the lateral geniculate nucleus particularly in the ventral part, as well as to the lateralis posterior nucleus. Widen and Ajmone-Marsan (1961) have cited evidence by Nauta that the lateral gyrus in the cat sends fibers to both dorsal and ventral parts of the lateral geniculate nucleus.

Niemer and Jimenez- Castellanos (1950), using strychnine neuronography, have described corticofugal responses ipsilaterally from stimulation of the posterior one-third of the lateral gyrus, chiefly in the S.C., but also frequently, responses were recorded in the pulvinar and in the anterior part of the lateral geniculate nucleus. Strychninization of the medial surface of the postero lateral gyrus produced responses in the dorsal part of the ipsilateral lateral geniculate nucleus, pulvinar, and superior colliculus. Widen and Ajmone-Marsan (1961) have also reported electrophysiologically definite corticofugal effects upon the lateral geniculate nucleus after stimulating the small area between the middle and posterior parts of the lateral and suprasylvian gyri, and also by similar studies (Ajmone-Marsan, and Morillo, 1961).

C. CENTRIFUGAL FIBERS TO THE SUPERIOR COLLICULUS

Subcortically, efferents from the lateral and posterior lateral gyri reach the brachium of the superior colliculus. Barris, Ingram and Ranson (1935), using the Marchi technique; Beresford (1961), using Nauta stain; have reported projection from the lateral and postero-lateral gyri to the ipsilateral superior colliculus, entering laterally the deep part of the stratum opticum and terminating in the superficial and intermediate gray strata.

Sprague (1963), utilizing Nauta-Laidlaw technique, has also shown that the critical areas studied terminated in different patterns within the colliculus, the anterior part of the occipital cortex projected to the postero-lateral half of the colliculus, and the posterior occipital cortex projected to the antero-medial half, terminating chiefly in optic and superficial gray strata. Fibers are found to project to the deep layers of the superior colliculus from the other neocortical areas. (Sprague, 1963).

The available data lead Garey (1965) to suggest that any part of the cortex related to a specific part of the retina is directly related to that part of the superior colliculus which is directly related to the same part of the retina. Apparently the fibers from the retina and the visual cortex end chiefly in the same layer. Fibers from the other cortical areas end predominantly in the deeper layers (Sprague, 1963), but the functional significance of this organization is not clear.

VI. THE CEREBELLAR VISUAL AREA

Sherrington's view of the cerebellum as the "head ganglion of the propioceptive system" was held to imply that this organ had to deal with proprioceptive information only until, exteroceptive projections were found almost simultanebusly by Snider and Stowell (1942, 1944), Dow and Anderson (1942), and Adrian (1943). Snider and Stowell (1944) should be credited with the unexpected discovery that not only tactile but also auditory and visual "information" is represented within the cerebellar cortex, although a few occasional observations of this kind had been reported previously by Gerard, Marshall and Saul (1936).

A. THE EXTENT OF THE VISUAL AREA

Snider and Stowell (1944) performed experiments on anesthetized cats, recording with moist wick electrodes, and using low intensity flashes from 3 w lamp placed 1 to 3 in. from the eye. Maximal responses were found in the lobulus simplex and tuber vermis (Larsall's lubules VI, H VI, and VII), although smaller and inconsistent responses were led occasionally from neighbouring areas, when chloralose anesthesia was used. Another important observation was that the auditory areas coincided very closely with cerebellar areas yielding a response to a flash of light. The visual responses, unlike the auditory, were only rarely obtained when the anesthetic was sodium pentobarbital. Consistent results were secured only when anesthesia was induced by chloralose or by a mixture of chloralose and sodium pentobarbital. Snider and Stowell suggested that the resistance to chloralose might ensue from an excitatory, strychnine-like action of this anesthetic. In all cases, there are two or three zones of maximal responses in the region of the second turn of vermis. The posterior zone occupies the caudal portion of the tuber vermis, and frequently extends into the rostral folia of the pyramid, sometimes even into the medial portions of the right paramedian lobule. A larger anterior zone of maximal response covers much of lobulus simplex and the rostral portions of the folium-tuber. The rostral zone may be divided into two parts by a band of responses of smaller amplitude.

Since, in these investigations, the possibility of recording cerebellar photic responses seemed to be dependent on a given experimental condition, namely the administration of chloralose, their significance was soon questioned. Gastaut, Naquet, Roger, and Badier (1951) suggested that these cerebellar potentials were similar in nature to the subconvulsive, "irradiated" responses which appeared simultaneously on the non-visual areas of the cerebral cortex (quoted by Fadiga and Pupilli, 1964). They also suggested that retinal impulses might reach the cerebellar cortex only in abnormal conditions, i.e., when the excitability of the tecto-cerebellar system had been increased by the injections of the convulsant drugs.

Whitlock (1952) was the first to show the possibility of evoking cerebellar photic responses in unanesthetized preparations. His experiments were performed on decerebrated pigeons, owls, and ducks. Auditory and visual receiving areas were found in Folia VIc (caudal declive), VII (folium and tuber vermis lobule), and VIII (pyramis). Whitlock emphasised that visual responses could be obtained only if the optic tectum was intact.

That the photic response of the cerebellar cortex was a normal phenomenon, although undoubtedly distorted and magnified by chloralose anesthesia, was shown by Fadiga, Pupilli, and Berger (1957). The responses of lobules VI and VII to photic stimuli were recorded in unanesthetised cats. They were decreased by cocanization, increased by injections of chloralose. These investigations have been carried out by means of flashes of white light; the flashing bulb was so placed as to obtain illuminations of 0.45-7.8 megalux at a distance of 30 cm. from the eye. Surface evoked potentials were led with conventional silver ball electrodes; for deep recording platinum 20 u wire electrodes were used. The topographical distributions were on declive and folium vermis when using weak stimuli. With stronger stimulation, photic responses could be led also from folia of the lobulus ansiformis (sublobule H VIIa). The responses were recordable from a much broader area while using chloralose anesthesia than in unanesthetized animals, so that for weak intensity stimulations, optic potentials were consistently recorded from the cerebellar hemispheres as well as from the vermis. Actually, according to these investigations the area responding to visual volleys encloses the whole dorsal surface of the cerebellum, with the exception of the most caudal portion of the uvula. Since only the dorsal surface has been explored in this connection, other regions cannot be absolutely excluded.

B. AFFERENT PROJECTIONS TO THE CEREBELLAR VISUAL AREA

Snider and Stowell (1944) were the first to suggest the possibility of direct transmission of optic fibers through tecto-cerebellar pathways. They recorded from the cerebellar cortex of cats, in which the whole cerebral cortex had been chronically ablated. The existence of tecto-cerebellar fibers has been observed in the lower mammalian species but not in the cat. The only positive findings from anatomical studies on higher mammalian species seem to be those reported by Ogawa and Mitomo (1938), and Larsell (1947) in the dog and human embryo (quoted by Fadiga and Pupilli, 1964). To our knowledge, thus far no author has ever described tecto-cerebellar fibers in the cat, where their existence is assumed by Snider and Stowell (1944) only on analogical considerations.

The hypothesis of indirect connections from the tectum through the pontine nuclei was suggested by Snider and Stowell (1944) themselves. The first leg of this route should be the tecto-pontine tracts, described in the cat by Rasmussen (1936) as running from the superior colliculus to the lateral regions of the ipsilateral pontine gray. Tecto-pontine fibers with similar course have also been traced in many mammalian and submammalian species, e.g., rabbit, Tasiro (1939); and opossum, Tsai (1925), (quoted by Fadiga and Pupilli, 1964). The second leg of the route can be envisaged in the ponto-cerebellar fibers, which in the cat preparations were seen by

Brodal and Jansen (1946), as originating from nearly all the pontine nuclei. These fibers enter the cerebellum via the middle peduncle and spread to the hemisphere as well as the vermis. Pathways depending on the cerebellopetal projections from the inferior olive and lateral reticular nucleus are another possibility. But these pathways can hardly be considered because of the lack of anatomical evidence (Walburg 1956, 1960).

Fadiga, von Berger, and Pupilli (1959 a,b) were able to show in the unanesthetized, curarized preparation that the cerebellar inflow of visual origin takes the route of the middle cerebellar peduncles. Their evidence is as follows They recorded electrical responses in the middle and superior cerebellar peduncles following primary optic pathway stimulation. The response of the middle peduncle always starts before the beginning of the positive wave evoked at the surface of the cerebellar cortex by the same stimulus. In the superior peduncle, on the other hand, the response appears later. In addition, the discharges evoked from the middle peduncle are unmodified after acute cerebellectomy, but in the superior peduncle, the dischanges are abolished in the operated cat. In chronic preparations, (Fadiga, Berger and Pupilli, 1959, b,c), after recovery from bilateral interruption of the middle cerebellar peduncles, neither photic nor electrical nerve responses are affected in eliciting corticocerebellar reactions before treatment with chloralose (quoted by Fadiga and Pupilli, 1964).

CEREBRO-CEREBELLAR PROJECTIONS

The existence of a definite relationship between cerebral cortex and cerebellar teleceptive projection areas was shown by Snider and Eldred (1948, 1951) and Hampson (1949). Upon threshold stimulation of cerebral auditory and visual areas, Snider and Eldred (1948, 1951) were able to record evoked potentials on the vermal portion of lobulus simplex and folium-tuber vermis of cats and monkeys, under a mixture of chloralose and sodium pentobarbital from a region practically coincident with the cerebellar audio-visual area as described by Snider and Stowell (1944). Supra threshold stimulation, on the other hand, was effective in activating almost all the dorsal aspect of the cerebellum. Hampson (1949), in the same animal species, obtained responses under sodium pentobarbital anesthesia, confined to the tuber vermis upon stimulation of the auditory cortex, but not from the striate cortex. The latency values observed ranged between 6 and 20 msec., depending upon the stimulated point, and on factors related to narcosis depth (Hampson, 1949; Jansen, 1957; and Snider and Eldred, 1951). They are slightly longer for the responses evoked by stimulation of the visual area than for those elicited by activating the auditory cortex. The two latency ranges probably indicate that cerebrally elicited impulses might follow two distinct paths on their way to the cerebellum, the one through pontine relays, and the other possibly through the inferior olivary nuclei (Jansen, 1957). The recent demonstration that olivo-cerebellar projections end as climbing fibers, associated with the view which regards all ponto-cerebellar systems as activating mossy fibers only, apparently supports this hypothesis. Electrophysiological evidence has been obtained by Jansen (1957) suggesting the possibility that the longer and shorter latency responses are respectively mediated by climbing and mossy fibers. Jansen (1957), however, shows that the long latency response component is unchanged by sectioning of restiform bodies in which the olivo-cerebellar fibers are known to course; furthermore, after lesions in the brachium pontis, both short- and long latency responses are abolished.

Fadiga and Pupilli (1964), in their review of cerebellar teleceptive responses, give conclusions about afferent cerebellar fibers of the visual area. They write: "A first wave of cerebellar activation is mediated by volleys originating from the tectal centers of the visual and acoustic systems. At least in higher mammals, under normal conditions these volleys seem to reach their termination along an indirect pathway, including precerebellar synaptic relays located somewhere in pontine nuclear formations. A second wave of cerebellar activation depends on the cortical output brought about by the specific response of the cerebral teleceptive projection areas, which are linked to the cerebellum through pathways also relaying at pontine level. Although no true point-to-point relationships can be detected, these linkages exhibit a focal arrangement in correspondence with the cerebellar lobules most heavily impinged upon by tectal volleys. The influence from striate area is in the main weaker than that originating in the cerebral area of auditory projection".

C. THE RELATIONSHIP OF THE CEREBELLUM TO EYE MOVEMENTS

The cerebellum may be regarded as a regulating device for the smooth execution of motor activity of the organism. Because of its reciprocal connections with the part of the brain directly concerned in motor activities, including the regions of the cortex concerned with voluntary movements, it is able to modify their activities continuously in the light of this information.

The control of eye movements, both reflex and voluntary, therefore involves this part of the brain.

STIMULATION EXPERIMENTS

In 1874 Hitzig first described eye movements following stimulation of the cerebellum (quoted by Dow and Manni, 1964). Ferrier (1886) reported that electric stimulation of the ansiform lobules in the cat gave upwards rotatory eye movements, the anterior vermis straight upward movements and the lateral portions of the anterior lobe downward eye movements. With experiments performed in intact, unanesthetized rabbits, Hoshino (1921) observed a horizontal deviation of both eyes toward the side stimulated. The response was abolished by cooling the cerebellar cortex, but not by bilateral labyrinthectomy (quoted by Dow and Moruzzi, 1958). Mussen (1934), studying both alert and anesthetized cats, reported that stimulation of the anterior vermis produced upward head and eye movements and the posterior vermis downward head and eye movements. Koella (1955, 1962) obtained downward head and eye movements by stimulation in the area of the lingula, uvula, and nodulus of alert anesthesized cats. However, in a number of other studies on both anesthetized and implanted cats and monkeys few patterned eye movements in planes other than horizontal have been described (Cohen et al, 1965).

Recently, Cohen et al (1965), using a concentric 20-gauge electrode with tip separation 2.0 mm. for the cerebellar cortex stimulation and a 0.5 mm tip separation for the cerebellar nuclei and white matter, stimulated the surface and interior of the cerebellum in alert, cervically-transected cats. A variety of patterned eye movements were produced. Horizontal eye movements were obtained from the tuber vermis and from the area of the fastigial nuclei. Straight upward and downward eye movements were evoked by stimulation of the midline vermis in the anterior and posterior lobes. Downward rotatory eye movements were induced from the region of interpositus nuclei, from the small area of overlying dorsal cortex, and from the lateral portions of the nodulus and uvula. Rotatory upward eye movements were evoked from ansiform lobes and from the region of dentate nuclei. These eye movements resemble those produced by semicircular canal nerve stimulation. They suggested that there is a topographic separation of the neural organizations which produce eye movement in various spatial planes in the cerebellum.

ABLATION EXPERIMENTS

Luciani (1891, quoted by Dow and Manni, 1964), who worked with dogs and monkeys, observed that after hemicerebellectomy the eye on the operated side was turned downward and inward, while the opposite eye showed deviation up and outward, yielding a picture of skew deviation. Slight nystagmus was also observed. After bilateral or total cerebellectomy there was ocular convergence in both eyes. Nystagmus following hemicerebellectomy is never long lasting. It disappears in a few days and is replaced by ocular deviation. It is therefore not generally thought of as a deficiency phenomenon. Luciani called it a dynamic manifestation of cerebellar lesions.

Concerning the cerebellar visual areas, data obtained in cats by Chamber and Sprague (1955) are of interest. In chronic experiments, they were able to observe that after bilateral ablation of tuber and folium their animals showed, apart from slight symptoms of the somatic sphere, also "difficulties in gauging distances properly when jumping and marked reduction in sensory attention". This impairment could be due to the reduction in startle response to loud noises and from the lack of attention to noises which, before operation, had aroused quick attention. Disturbances related to the visual system were observed. These are: "marked tendency for visual attention to become fixed", and "slight responses to visual cues". The auditory disturbances were remarkably stable but disturbances related to the visual system, on the other hand, were limited to the early part of the post operative period and progressively disappeared.

EXPERIMENTAL METHODS

EXPERIMENTAL METHOD

The general method has been basically the same throughout the whole series of experiments. This consisted essentially of an exploration of the lateral geniculate nucleus, superior colliculus and cerebellar visual area of the cat, and the superior colliculus of the baboon with a monopolar microelectrode held in a stereotaxic machine; visual stimulation was applied to the retina. In one group of experiments, a cooling device was used to study the influence of the visual cortex on the superior colliculus of the cat.

I. PREPARATION OF ANIMALS

Eighty four cats, whose body weight ranged from 2-4 kg.; and 5 baboons of 4-8 kg. were used in this study.

A. ANAESTHETIC METHOD

CAT

The cats were anaesthetised with trilene (trichlorethylene) pumped into a small box, as it was thought to be important to avoid a stage of excitement. When unconscious the cats were removed from the box and were then given chloralose (80 mg./kg. body wt.) intravenously into the exposed leg vein.

It was found that before injecting chloralose the anaesthetic level had to be controlled by ether inhalation. This usually gave a satisfactory level of anaesthesia for 9-12 hours.

In some experiments on the superior colliculus, the initial anaesthetic, nembutal (sodium pentobarbitone; Abbott Laboratories) 40 mg./ kg. body wt. was used intraperitoneally. It was found that there were no differences between these two anaesthetics in the electrical activities of the superior colliculus.

Supplementary doses of anaesthetic were given to maintain a desirable level of anaesthesia, either a half dose of chloralose intravenously every 4-8 hrs., or nembutal, 10 mg. intravenously every 2-3 hours.

In the experiments on the cerebellum, chloralose was used exclusively for initial or supplementary doses. Barbiturate anaesthetics were found to prevent or abolish the visual responses.

BABOON

The baboons were put in a small cage and the trilene was pumped in slowly until the animal became drowsy, then ether was administered. The moment the animal appeared to be unconscious, the chloralose (80 mg./kg. body wt.) was given intravenously. This usually gave a satisfactory level of anaesthesia.

Supplementary anaesthetics were given by one of the following methods:-

1. Half dose of chloralose intravenously.
2. Pentothal (thiopentone sodium) in 0.9% NaCl by intravenous drip.

B. OPERATIVE PROCEDURE

After the animal had been anaesthetised, its trachea was cannulated. The conjunctivae were anaesthetised with xylocaine (lignocaine HCl), and the lids were sutured together to prevent drying during the operative procedure. The animal body temperature was closely held to 38°C. by means of an electric heating blanket regulated by a thermister placed in the rectum. Continuous blood pressure recording was monitored by a strain-gauge manometer in all the baboons, but only in some of the cats.

The external auditory meatus was split downward and forward to allow accurate insertion of ear plugs into the bony meatus. The lids were reopened and four silk ligatures were put into the limbus. A lateral canthotomy was found necessary for subsequent introduction of a brass ring and its manoeuvre.

The skull was exposed by a cruciate skin incision. A hole was bored by a high speed dental drill. Bleeding from diploe was arrested with plasticine. The exposed dura was covered with cotton wool soaked in N.S.S. and the skin apposed by a suture until the animal was mounted in the stereotaxic machine.

For the experiment on the lateral geniculate nucleus of the cat, a hole was bored on the left dorsal surface of the skull. The hole extended from about 5 mm. posterior to the bregma to about 1.0-1.5 cm. long, antero-posteriorly; and from a few mm. lateral to the sagittal suture to about 1.0 cm. wide, medio-laterally.

For the cat's superior colliculus, the hole was drilled on the same side of the skull but was more posterior and medial, being about 10 mm. behind the bregma for the anterior margin, and a few mm. across the midline for the medial border. In some experiments, the center of the hole was marked when the animal had been already fixed in the stereotaxic apparatus, in order to use the Clarke-Horsley landmarks. By this method a small hole could be drilled over the presumed position of the superior colliculus with accuracy.

In baboon experiments, in order to reach the superior colliculus with some degree of accuracy and to minimize skull opening, it was necessary to mark the center of the hole after the animal had been fixed in the stereotaxic machine.

After surgery, the animal's head was then fixed in the stereotaxic apparatus, modified so as not to obstruct the visual field, with ear plugs and the lower orbital margin in the same horizontal plane. The skin flaps were raised and tied with a metal ring, and the dura was opened under the dissecting microscope. Cerebral pulsation was avoided by the use of 3% agar, which was heated to its boiling point in a water-bath and then gradually cooled to a temperature of 42°C. before being poured into the cranial hole.

Plasma substitute, dextran, was usually given, if the animal had lost a considerable amount of blood, in order to maintain the circulating blood volume. Fluid and electrolytes were also given. The total volume of 40 ml./kg. body wt./day was divided into 4 parts of 5% glucose and one part of normal saline solution. An antibiotic was given to prevent infection in prolonged experiments.

C. METHODS OF FIXING AND CENTERING THE EYE

The stereotaxic apparatus was arranged so that the right eye was at the center of a modified Aimark perimeter whose arm had a radius of 33 cm.. The scleral sutures were tied to a brass ring so that the slit of the constricted pupil was vertical. The pupil was dilated with 1% atropine sulphate to permit observation of the fundus. Cat's eyes are usually 1 D or 2 D hypermetropic when atropinized

(Bishop et al, 1962). A plastic contact lens was specially constructed having the inner radii of curvature of 8.5, 9.0 mm. and with the optical power +4.5 D in order to focus at 33 cm., this being the distance between the perimeter and the eye.

In the cat, the eye was moved by adjusting the brass ring until the projection of the blind spot was 16-18° to the temporal side and on the radius 15° above the horizontal meridian, observed by a Fison indirect opthalmoscope. An adjustable angle mirror was put over the center of the perimeter and the fundus was observed by an opthalmoscope reflected in the mirror. The area centralis can be recognised as a green pigmented area, and devoid of blood vessels. Small adjustments of the position of the eye were sufficient to bring the visual axis to the center of the perimeter. The receptive fields of the two eyes for a single point in the visual cortex were found to coincide within less than 2°, when this method was used.

In the baboon, the eye was centred by determining the projection of the blind spot. The brass ring was adjusted until the blind spot was 15° to the temporal side on the horizontal meridian. This does not, however, determine the visual axis with accuracy. In the later experiments, one electrode was placed on the most lateral anterior part of the superficial cortex in order to record the visual response from the cortex subserving the fovial region. By moving the brass ring, the eye was then adjusted until the light at the center of the perimeter gave the largest and earliest responses from this electrode.

II. STIMULATING AND RECORDING EQUIPMENT

A. STIMULATING EQUIPMENT

Various kinds of stimuli - neon-tube, card-board, a perimeter giving a spot of light, and a stimulator giving a light-bar - were used as the visual stimuli.

In mapping experiments, the field was explored with a neon-tube 5 mm in diameter which flashes for about 5 msec. This provided too much light for exact localisation, and final mapping was done with a spot of light from the perimeter. Black and white cards of varying size and shape were found to be useful stimuli.

PERIMETER

The perimeter (Aimark) gave a circular spot of white light of 1, 3, 5 and 10 mm. in diameter of the arc. The density filter wheel contains one free aperture and three neutral filters of optical densities 0.6, 1.2 and 1.8, transmitting therefore 1/4, 1/16, and 1/64 of incident light respectively. With the free aperture in position the brightness of the white testing stimulus is approximately 41.16 cd/m^2 , and consequently 10.29, 2.57, and 0.65 cd/m^2 when the filters are interposed. A transistor photocell was placed beyond the shutter,and its excitation by the stimuli provided synchronization for the cathode ray tube sweep at 'on', 'off' or 'on and off'.

LIGHT - BAR STIMULATOR

A 500 w. lamp and condensor lens projected a bar of light of variable size via a plane mirror mounted on a pen-motor. The velocity and repetition frequency of the mirror were controlled by the oscilloscope time base. A Dove prism served to rotate the direction of the moving stimulus.

B. THE RECORDING EQUIPMENT

THE MICROELECTRODES

The microelectrodes used have been monopolar tungsten needles as described by Hubel (1957) with some modifications. These were made from tungsten wire 0.5 mm. in diameter. Sharpening of the electrodes by electropolishing in a saturated solution of sodium nitrite with AC at about 10 V was performed until the terminal was very fine. One changes to 1.5 -3.0 V and puts the very fine terminal in the bath to cut it off.

Coating:- the electrode with satisfactory shape and tip (about 1 u) was cleaned in acetone or trilene (trichlorethylene). In the earlier experiments, electrodes were insulated with one coat of INSL-X-E 33N clear varnish (The INSL-X company Inc., N.Y.). The INSL-X was thinned with chloroform to the consistency of honey. The electrodes were immersed in the coating fluid with the point upright, and were gradually raised from the varnish and allowed to dry in room temperature, still point upright, for at least 24 hrs, before testing.

In the later experiments, the electrodes were insulated with "Bakelite" lacquer, as it was found that this kind of varnish was stronger and lasted longer than the clear varnish. The cleaned electrodes were immersed in Bakelite with the tip down and slowly raised. Three coats in all were applied to each needle, and between each coat the electrode was baked by blowing hot air over the needle, slowly increasing the temperature to about 250°C. and maintained in that temperature for 1 min.

Testing:

The procedure consisted of passing a square wave of 100 mv. and 20 msec. duration through the electrode in N.S.S. medium and finally feeding through the cathode follower to display on the oscilloscope; the circuit was shorted with 10 megohms between grid and earth. The circuit diagram is shown in Fig. 1. The proper impedance electrode for single unit recording showed the shape of wave-form (a), consisting of fairly rapid falling phase to a D.C. level just above the base line, too high impedance electrode gave the shape (b), or too low impedance, (c). About half of the electrodes made had too high impedance, and it was necessary to break off the tip by briefly passing a small amount of current for 1.5 v battery. This was done while watching the waveform during testing.

The electrodes were also tested by applying a sine wave, 1000 c/sec, 100 mv in amplitude from a signal generator and the resistance was measured by using the varying values of known resistors. The good electrode for single unit recording was found to have an impedance about 1 megohm.

THE ELECTRONIC APPARATUS

The electrode bridge of the stereotaxic machine carried three micromanipulators, permitting movement of the electrode in three planes to an accuracy of 5 microns in the vertical plane.

The activity was displayed by amplification of the voltage between the tip of the microelectrode and the indifferent electrode buried in the neck muscle. A cathode follower and a three stage R.C. coupled amplifier with variable time constant were used. The output from the amplifier was fed in parallel to a display oscilloscope, loudspeaker, and to the oscilloscope of a camera unit.

A monitoring loudspeaker was an important part of the equipment; it is much easier to identify by ear a response against a back-ground noise-level than it is to pick out the same response when seen only on an oscilloscope. The loudspeaker permits the recognition of faint responses, too small to be either seen or photographed.

Two double beam cathode ray tubes were included in the photographic unit in which the cellular activity, stimulus signal, and time signal could be photographed.

III EXPERIMENTAL PROCEDURE

Apart from the general experimental methods which have been already described, the special experimental procedure of each series of experiments is described in detail.

CAT

A. THE LATERAL GENICULATE NUCLEUS

The stereotaxic atlas by Jasper and Ajmone-Marsan (1960) was used in this experiment. The center of the lateral geniculate nucleus was found at 6 mm. anterior to the intra-aural plane, 9 mm. lateral to the midline, the same position given in the atlas.

In searching for the secondary area of the lateral geniculate nucleus; the electrode was lowered to aim at the center of the main nucleus, being about 12 mm. from the surface of the cerebral cortex; secondly, the electrode was shifted medially and posteriorly for the secondary area of the upper field (Seneviratne, 1963), and medially for the secondary area of the lower field. Single units were also studied in this experiment.

B. THE SUPERIOR COLLICULUS

For the earlier experiments, the stereotaxic atlas of Jasper and Ajmone-Marsan (1960) was used. In the latter experiments, the center of the superior colliculus was found at the intra-aural plane, 3 mm. lateral from the midline. This means that the superior colliculus in this experiment was a little posterior to the position given in the atlas. During the advance of the electrode to the superior colliculus, the electrode recorded the cellular activity of the gray matter of the dorsal and ventral surfaces of the cortex; and when the electrode tip was near the surface of the superior colliculus, a small diphasic wave which was fairly localized in the visual field by a neon light, could be obtained; with further downward movement of the electrode the surface laywr of the colliculus was reached; this being characterised by an abrupt change both in the quantity and the quality of the responses; the low pitched sound of the biphasic response changed to a higher pitched crackle of cells with a high amplitude biphasic wave superimposed by cell spikes.

In mapping experiments, for searching the receptive field, a short duration neon flash was used, this being triggered by the sweep of the display oscilloscope; exact localization of the receptive field on the perimeter arm was obtained by a 1 mm spot and small pieces of card-board subtending 1/2° at the eye. The position of the eye was checked frequently throughout the experiment, and at its termination, to ensure that the visual axis still remained at the center.

For unit studies, after the electrode had touched the surface of the superior colliculus, it was advanced very slowly, 10 u at a time, searching for the visual response or the spontaneous activity. Units were studied from the surface to the deep part till cessation of the visual response. Correlations between units recorded and the layers of the S.C. were done by making electrolytic lesions and calculating back for the required depth.

COOLING EXPERIMENT

In the experiments designed for the study of the influences of the visual cortex upon the S.C., the cooling device consisted of a probe with a shape of metal foot 2 x 5 mm in size. This was cooled by the expansion of the compressed gas (propane) at the tip of the probe (Dondey et al., 1962). The temperature of the cooler was controlled by an adjustable knob at the top of the probe, in which the rate of flow of gas was varied. The temperature was measured by means of a thermocouple attached to the metal foot.

The animal was prepared for recording as usual but the cooler was placed on the medial wall of the visual cortex with the center at 1 mm anterior to the intra-aural plane. This was expected to cool the visual cortex (visual I) subserving about 10°-15° out on the radius of 200°-240°

(Whitteridge, unpublished observations). The cortical area in contact with the cooler was mapped before the cooling experiments were performed. The cortex was cooled down to about 10°C., for about 2-10 min., when the single unit which was recorded from a corresponding point, was obtained in the superior colliculus. Visual responses were studied in the superficial as well as the deep part of the superior colliculus before and after cooling the visual cortex. The experimental arrangement is shown in Fig. 2.

C. THE CEREBELLAR VISUAL AREA

In the ordinary Clarke-Horsley plane, the cerebellar visual area can be reached by a posterior approach. It was found that the arrangement of the plane of the electrode by tilting 60° from the vertical line gave a satisfactory approach to the surface of the folium and tuber vermis. (Fig. 3).

After the cat had been fixed in the stereotaxic apparatus, by using the external occipital protuberance as the center of the skull opening, the bone was drilled to about 5-7 mm. anterior to the foramen magnum, posteriorly to about 2 mm. behind the lamdoidal suture by removing the posterior half of the interparietal bone, anteriorly. The hole was also extended to about 6-7 mm. from the midline on both sides laterally. Care had to be taken not to remove the bone too far posteriorly, at least 5 mm. should be left in order to permit good fixation of the agar on the bone; the head mounted in the head holder was rotated downward until the folium and tuber vermis came in to view horizontally. Immediately after the dura was removed, the cranial hole was sealed by 3% agar. The head was rotated back to the original position after the agar had set.

Owing to the complexity of the cerebellar cortex, especially the tortuous shape of the vermis, the outline of the exposed brain was drawn under camera lucida or under direct vision. This was found to be a good guide for explorations.

In searching for the visual responses, the neon lamp was tried in a few experiments; the visual responses were obtained only occasionally at the first time of moving the stimulus into the receptive field. In the latter experiments, moving stimuli, including card-board and a light-bar from the stimulator, were used. The extent of the visual area was explored on the surface as well as the deep part of the cortex. In single unit studies, the moving card for seeking the unit responses was found to be a useful stimulus before quantitative studies with a light-bar from the stimulator, in which the velocity, direction, and repetition frequency could be controlled.

BABOON

A. THE SUPERIOR COLLICULUS

The stereotaxic atlas of the macaque was used, because the atlas of the baboon was not available. The center of the superior colliculus in the C-H plane is 3 mm. anterior to the inter-aural plane (Clarke and Henderson, 1920). Using the guide from this atlas, it was found that the center of the baboon's S.C. in the C-H plane was not far from that in the macaque.

In the earlier experiments, the C-H co-ordinate was used to explore the superior colliculus. In this plane, the surface of the superior colliculus was very oblique or nearly vertical. In the later experiments, the baboon's head was tilted by 30°. The center of the superior colliculus, as calculated from the atlas of the macaque mentioned above, was about 7-8 mm. anterior to the inter-aural plane. This was near the actual position in these experiments. The experimental arrangement is shown in Fig. 4.

IV HISTOLOGICAL METHOD

At the end of the experiment the animal was killed with an overdose of nembutal and perfused through the ascending aorta with 10% buffered formalin in normal saline. The brain was fixed, without removing the head from its stereotaxic head holder. On the next day the relevant block of brain was removed, using a knife-blade moving transversely or longitudinally, depending upon the plane of the section wanted, and operated by the manipulator which had held the recording electrodes.

The brain was cut at 100 u on a freezing microtome. This thickness of section gave the best results, shrinkage and distortion during fixation being minimal. The sections were mounted on slides coated with chrome alum-gelatin solution, and dried on the hot plate. The sections were dehydrated by washing in ascending grades of alcohol. They were stained for 15 min. in 1% toluidine blue ("Michrome" Edward Gurr); and differentiated in Gotthard's differentiator, after dehydration in alcohol, and finally cleared in absolute alcohol and xylol and mounted in D.P.X. mountant (B.D.H.).

The electrode tracks were traced by drawing the outline of brain from the slide projector which was adjusted to give a linear magnification of X 10 or X 15. Superimposition of the drawings of adjacent tracks gave a reliable method of reconstructing the entire extent of the electrode tracks.

In lateral geniculate experiments, it was found that the sections cut transversely gave the better view of the nucleus. The projection of the "dorsal surface view" was obtained by direct measurement of the extent of the nucleus, anterior and posterior to the tracks, and by determining the positions of the secondary visual area in relation to the main nucleus.

For mapping experiments on the superior colliculus of the cat the brain was cut transversely. The plane projection of the surface area of superficial cell layer, stratum griseum superficiale, was made by measuring the length of a layer on each section. This length represented the flat surface of the superficial cell layer, medio-laterally. In order to flatten the colliculus antereo-posteriorly, a small hole was drilled antereo-posteriorly through the block of fixed brain parallel with the plane of the dorsal surface of the superior colliculus, and the distances from the hole to the surface in every section were used to construct the antero-posterior curvature. In some experiments, the flattening of the antero-posterior curvature was obtained by parasagittal section of the superior colliculus on the opposite side. The length of the superficial cell layer of a section was plotted on graph paper and the positions of the electrode tracks were marked. These enabled the adjacent sections to be aligned, one with respect to the next. By this method, the surface of the superior colliculus can be flattened both medio-laterally and antero-posteriorly.

Owing to the oblique surface of the superior colliculus of the baboon in relation to the plane studied, it was necessary to cut the brain parasagittally. By following the above procedure for the cat, the plane projection of the surface of the superior colliculus was also made.

In the experiments on the cerebellum, the sections were cut parasagittally, and correlations between units recorded and the anatomical positions were also studied.

ABBREVIATIONS USED IN THIS THESIS

CL = Experiment on cat's lateral geniculate nucleus
CS = Experiment on cat's superior colliculus
MS = Experiment on baboon's superior colliculus
L.G.N. = Lateral geniculate nucleus
N.I.M. = Nucleus interlaminalis medialis
S.C. = Superior colliculus
S = Superior
I = Inferior
M = Medial
L = Lateral
A = Anterior
P = Posterior
N.S.S. = Normal saline solution (0.9% NaCl)

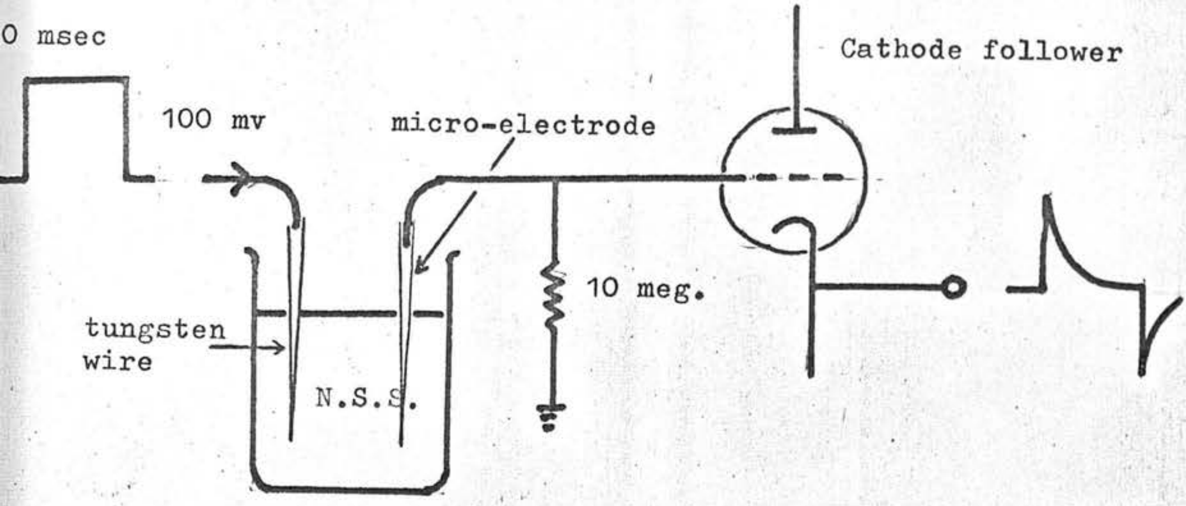
Fig. 1

Circuit diagram to show the method of testing a micro-electrode and the wave-forms obtained.

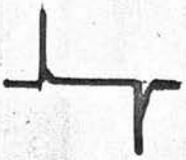
(a) Proper impedance for isolation of unit

(b) too high

(c) too low


0 msec
100 mv
micro-electrode
Cathode follower
10 meg.
tungsten
wire
N.S.S.


(a)


(b)

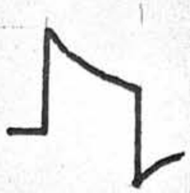

(c)

Fig. 2

Experimental arrangement for recording from the cerebellar visual area; showing the cat in stereotaxic apparatus, electrode holder tilted 60° and perimeter used.

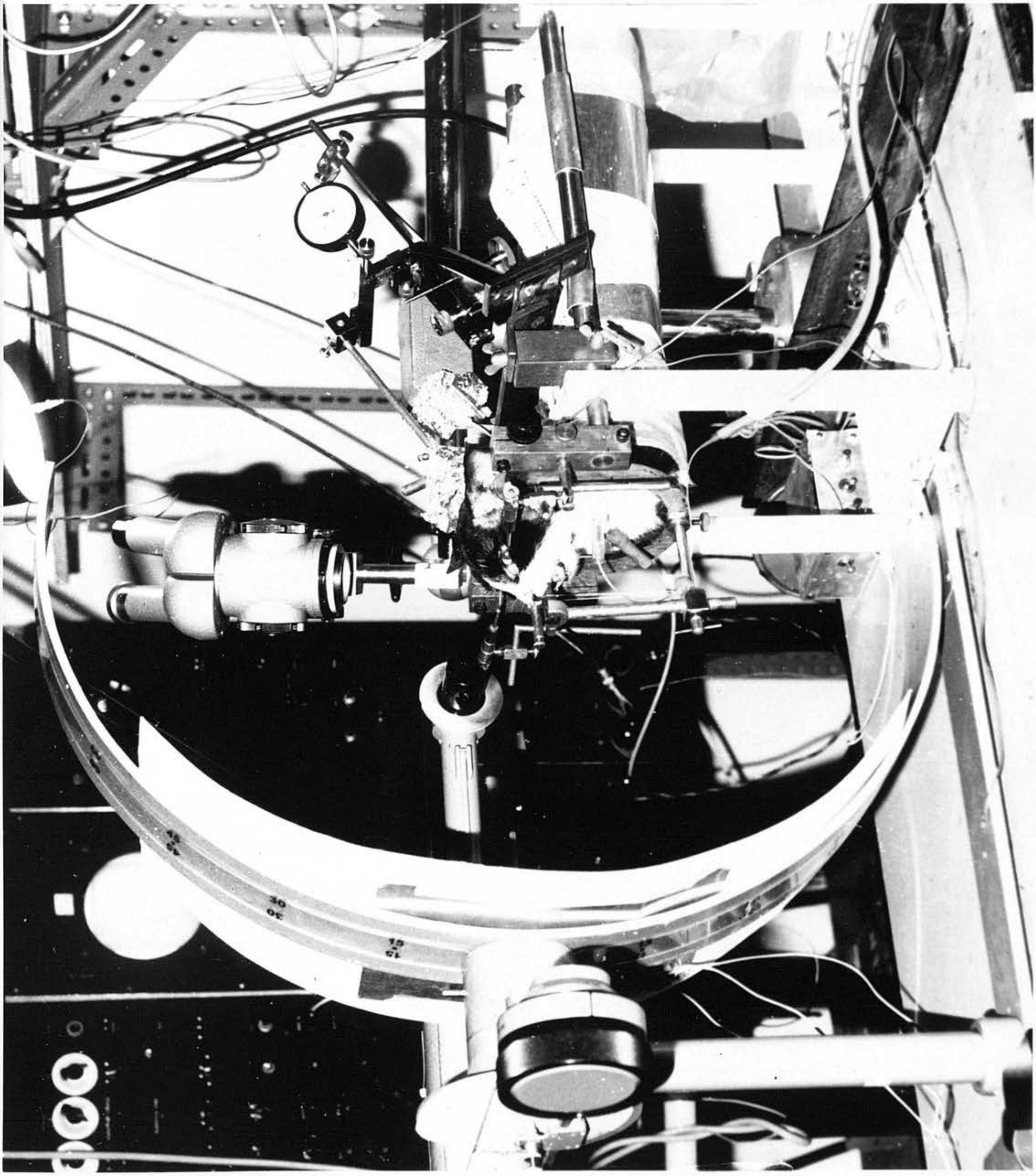

45
30
15

Fig. 3

Experimental arrangement for cooling experiments; the cooling device, shown on the left of the electrode holder,is connected with a propane cylinder and tele-thermometer; the position of the cat in the stereotaxic head holder, with eye-rings, jaw clamp and electrode-bridge assembly in situ.

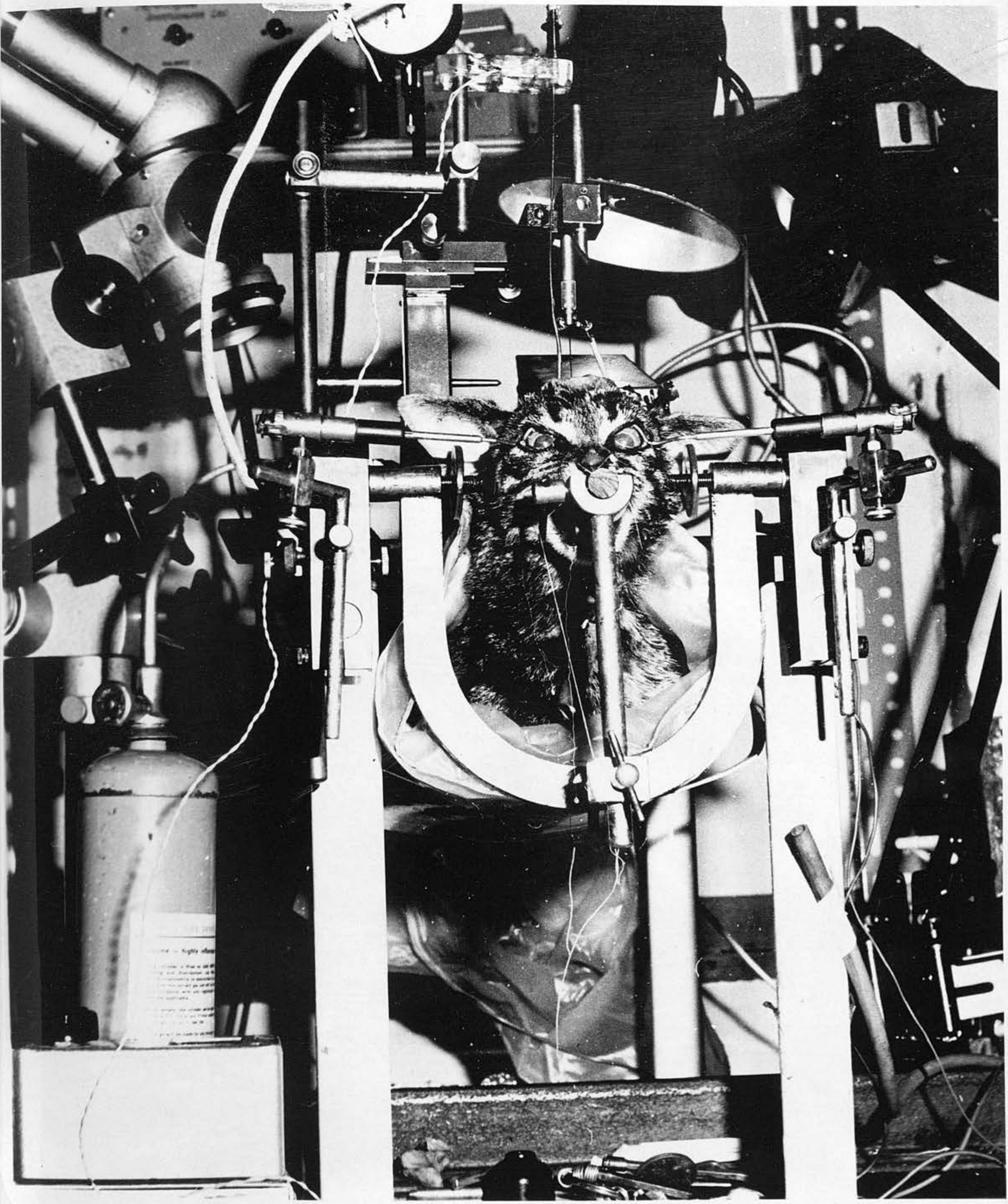
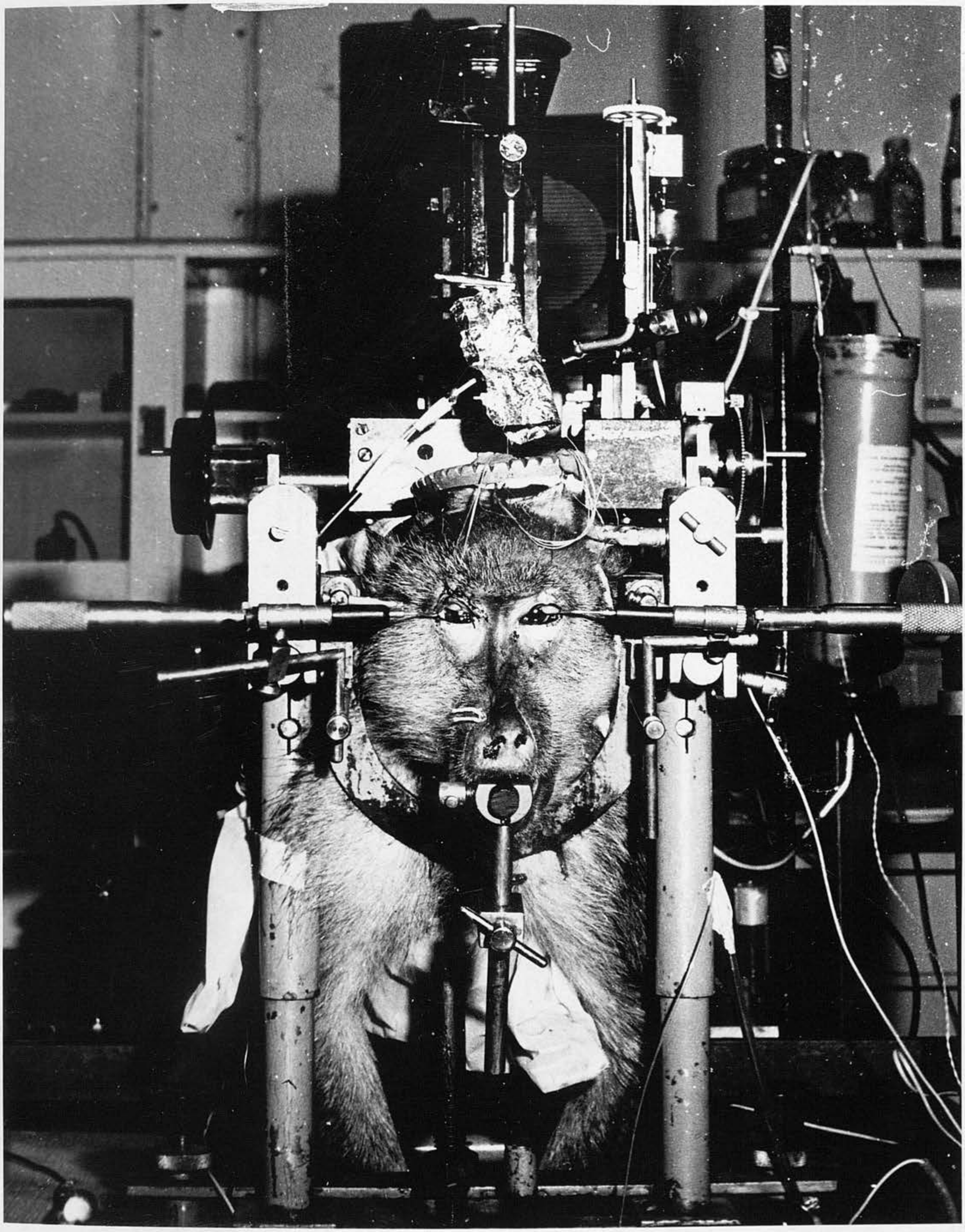


Fig. 4

Baboon in stereotaxic head holder with jaw-clamp, eye-rings and electrode-bridge assembly, in situ.



EXPERIMENTAL RESULTS

THE NUCLEUS INTERLAMINALIS MEDIALIS OF THE L.G.N.

I. THE NUCLEUS INTERLAMINALIS MEDIALIS OF THE L.G.N.

Out of more than 20 experiments, the results of 8 successful experiments are shown as the projections of the 2^{ry} visual area onto the N.I.M. in relation to the main nucleus of the L.G.N., with the drawings of the cross sections showing the electrode tracks and the sites of recordings on the N.I.M. (Fig. 7, 8, 9 and 10).

A. GENERAL CONSIDERATIONS

The nucleus interlaminalis medialis (N.I.M.) is a relatively small group of cells, being about 4 mm. in the antero-posterior direction and 4 mm. in the dorso-ventral direction. It is about 1 mm. wide posteriorly and 0.6 mm. anteriorly, as measured by Stone and Hansen (1966). The shape of the N.I.M. varies considerably from animal to animal as well as in size, as shown by the drawings of the cross sections from 8 experiments (Fig. 7 to 10). In toluidine blue stained sections, it was possible to distinguish the N.I.M. from the surrounding structures (Fig. 5 and 6), but in some histological sections it was difficult to draw the outline of this nucleus. It was difficult to insert an electrode for the first time into this nucleus, so it was necessary to aim at the main nucleus of the L.G.N. as a guide and then to change the electrode position to the N.I.M. The shifting of the receptive field laterally away from a vertical meridian in the expected anatomical position of the N.I.M. as the electrode was moved medially was used as a criterion for the identification of the 2^{ry} visual area. However, a histological verification of the electrode position was found to be an essential procedure in this study.

As seen in Fig. 8, three electrode tracks are shown in each experiment. (a and b). In (b) the most lateral electrode track recorded from layer A and the location of the receptive field was on 15°-142°. As it was moved medially the receptive field changed to 63°-97° (near the vertical meridian, 90°). The localization of the receptive field of the most medial electrode, 48°-116°, was shifted again but in the reverse direction from the vertical meridian. The electrode track was subsequently found to penetrate the N.I.M.. This technique of identification can be used when recordings are made in the 2^{ry} visual area of the upper field quadrant because the N.I.M. at this region is attached to the main nucleus medially. When recordings were made in the anterior part of the N.I.M., an additional criterion has to be used, because the large part of the N.I.M. in this region is situated under the medial edge of the main nucleus. Recordings from the N.I.M. were obtained when the electrode had penetrated the different layers of the

L.G.N. as seen in Fig. 9a and 10b. Most of the localizations of the receptive fields were obtained from multiunit recordings.

B. THE RETINOTOPIC ORGANIZATION ON THE N.I.M.

The results of the experiments have confirmed the electrophysiological studies of Seneviratne and Whitteridge (1962), and Seneviratne (1963) that the upper visual field is represented on the posterior part of the N.I.M. in the posteromedial curl, and have extended the observations into the anterior part of the N.I.M., which has been found to contain the representation of the lower field.

Several attempts were made to map the retinotopic projection onto the N.I.M.. None of these were successful in obtaining enough points in order to construct the projection map. Only a few points of localizations in the N.I.M., as verified histologically, were obtained in each experiment. However, the results of all experiments were taken into consideration for construction of the projection map.

The retinal representation onto the N.I.M. seems to be the mirror image of the 1^{ry} visual area of the main nucleus of the L.G.N.. By examining the points of localization of the drawings of transverse sections, the responses from the N.I.M. are on the meridians corresponding to the localizations on the main nucleus.

In the region of the postero-medial curl, the points of localization in the visual field recorded from the N.I.M. were on the peripheral field, up to 60° or 80° from the center of fixation and on the radius near the upper vertical meridian (0°-90°). As the electrodes were lowered down along the N.I.M., the localizing points were moved in gradually to the center of fixation and at the same time moving out from the upper vertical meridian (0°-90°) towards the horizontal meridian (0°-180°). Thus the retinotopic organization of the upper field on the posterior part of the N.I.M. shows some arrangement in dorso-ventral as well as antero-posterior direction which is consistent with the anatomical configuration of the N.I.M. in this region viewing as a plate of cells placed vertically on the medial side of the L.G.N.

The condition was different in the anterior part of the N.I.M., where the nucleus has the representation of the lower field. The points of localization were moved away from the center of fixation and towards the lower vertical meridian (0°-270°), but with smaller scale than in the posterior part of the N.I.M.. In addition, the receptive fields were also moved towards the lower vertical meridian (0°-270°) at a fast rate, when the positions of the electrodes were inserted laterally. Here again, some retinotopic organizations in the dorso-ventral and medio-lateral directions do exist, and correspond to the thin band of cells situated under and along the medial side of the L.G.N.

For the responses in the sectors near the horizontal meridian (0°-180°), an electrode placed laterally, recorded the response near the center of the visual field (Fig. 10 b, right), whereas the medially placed electrode recorded the activity farther away from the center (Fig. 9b, A) up to 70° from the center of fixation in the medial position. (Fig. 10a, left). The retinotopic organization no longer shows an arrangement in dorso-ventral dimension, but it seems to show an arrangement in medio-lateral dimension. The shape of the N.I.M. in this region also shows an increase in the medio-lateral dimension, whereas the dorso-ventral dimension has reduced.

Taken together as a whole, the upper vertical meridian (0°-90°) appears to begin from the posterior end of the N.I.M. and runs forwards and downwards gradually to the center of fixation, which is situated somewhere just under the medial edge of the main nucleus of the L.G.N. after continuing its course as the lower vertical meridian (0°-270°), it still proceeds anteriorly but moving laterally to be situated under the anterior part of the L.G.N. For the sake of simplicity, the N.I.M. can be viewed as a plate of cells which has twisted from the vertically orientated into a horizontally orientated position in the middle of its course. The diagram of the retinotopic organization onto the N.I.M. is shown in Fig. 11.

C. THE EXTENT OF THE VISUAL FIELD

The composite results of 11 experiments are illustrated, showing the points of localization in the visual field. (Fig. 12). The extent of the visual field as plotted in these experiments has shown that the upper visual field extends to about 70°, but only 30° or less in the lower field. The temporal extent is up to 80° in the horizontal meridian. The extent of the visual field plotted is not regarded as significant because some part of the N.I.M. has not been explored.

Most of the responses were observed from the contralateral eye. On only a few occasions (5 points) were they observed from the ipsilateral eye. The responses from both eyes have not been observed. All the points of localization were in the peripheral or pericentral visual field. The central visual field representing the area centralis has not been found.

D. SINGLE UNIT OBSERVATIONS

In the course of mapping experiments, some single units have been observed. The latencies of the sample of these units were measured by presenting a neon flash at the perimeter arm, comparing with the latencies to the main nucleus of the L.G.N. (Fig. 13b to g., and 14a, b). All the latencies are within the same range.

The units recorded from the N.I.M. had 'on' and 'off' center fields (Fig. 14 c). Two units showed prolonged after discharges similar to the behaviour of units in the lamina B described by Seneviratne (1963).

The sizes of the receptive field were also measured, and varied from 5°-20° in diameter. One unit had a very large receptive field, being about 60° across. The characteristics of units are shown in Table 1.

All sections of cat and baboon's brains, cut at 100 u, and stained with toluidine blue.

Fig. 5

(a) Photomicrograph of cat's brain section, to show position of the L.G.N. and 3 electrode tracks passing through the nucleus. Note; the nucleus interlaminalis medialis is penetrated by the most medial electrode track. (CL 14).

Section magnification X 4.6

(b) Photomicrograph of transverse section of cat's L.G.N., to show course of 3 electrode tracks. The nucleus interlaminalis medialis, recognized as a group of cells separated from the posterior nucleus medially and the main nucleus laterally, is passed by the medial electrode track. (CL 14).

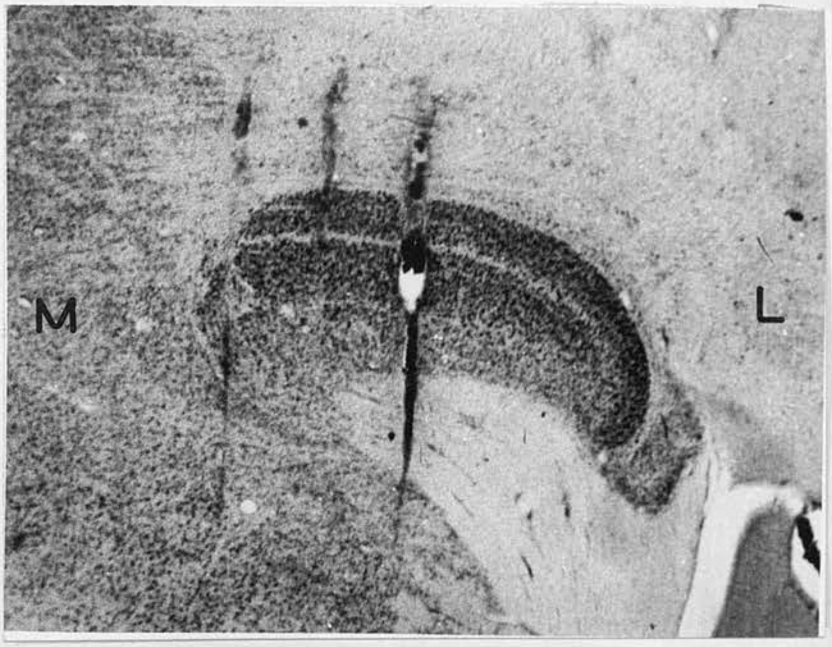
Section magnification X 14

(c) Transverse section, left L.G.N., to show the medial 3 electrode tracks passing through the nucleus interlaminalis medialis. (CL 14).

Section magnification X 23

a

b



c

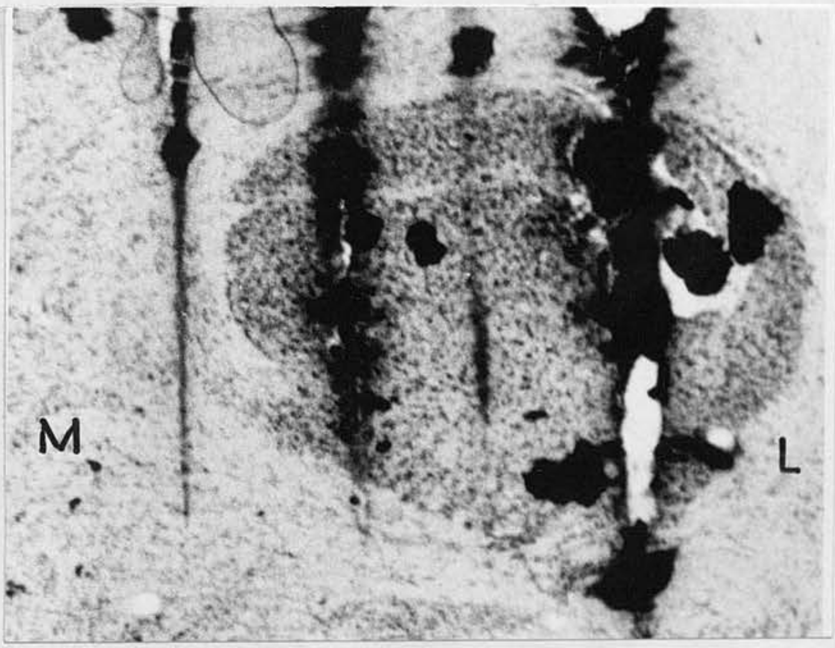


Fig. 6

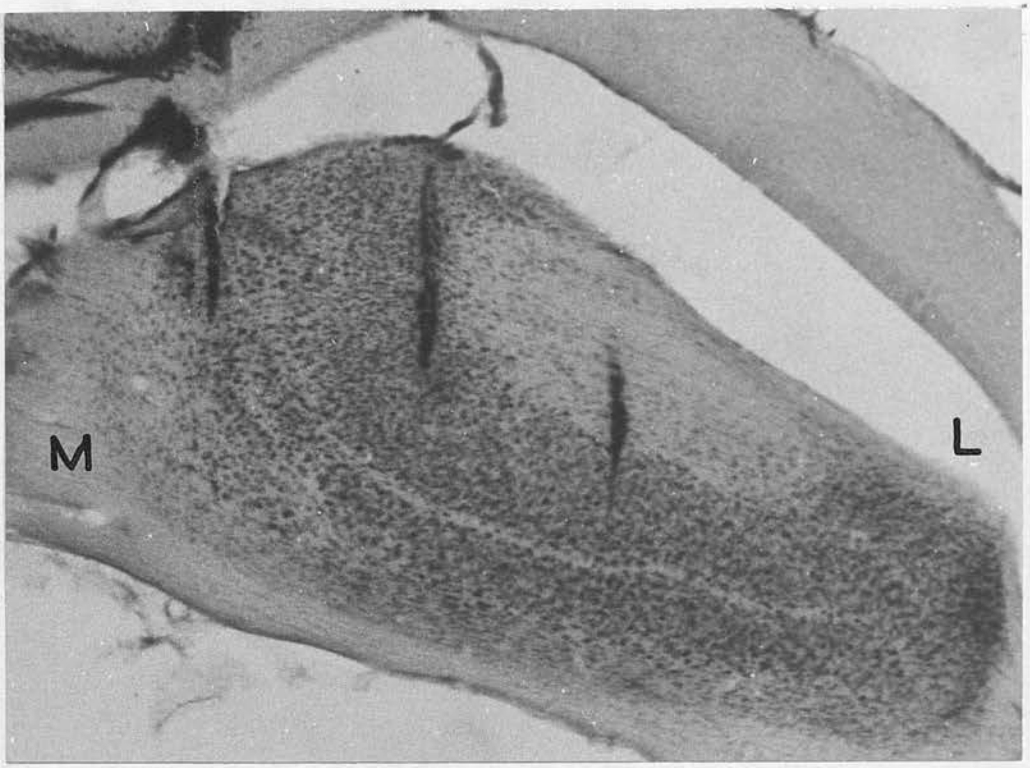
(a) Photomicrograph of transverse section of L.G.N., to show 3 electrode tracks; medially, the characteristic appearance of the nucleus interlaminalis medialis, being penetrated by the most medial electrode track. (CL 24).

Section magnification X 25

(b) Transverse section of L.G.N., to show 2 electrode tracks passing through the nucleus interlaminalis medialis. (CL 6)

Section magnification X 18.

a



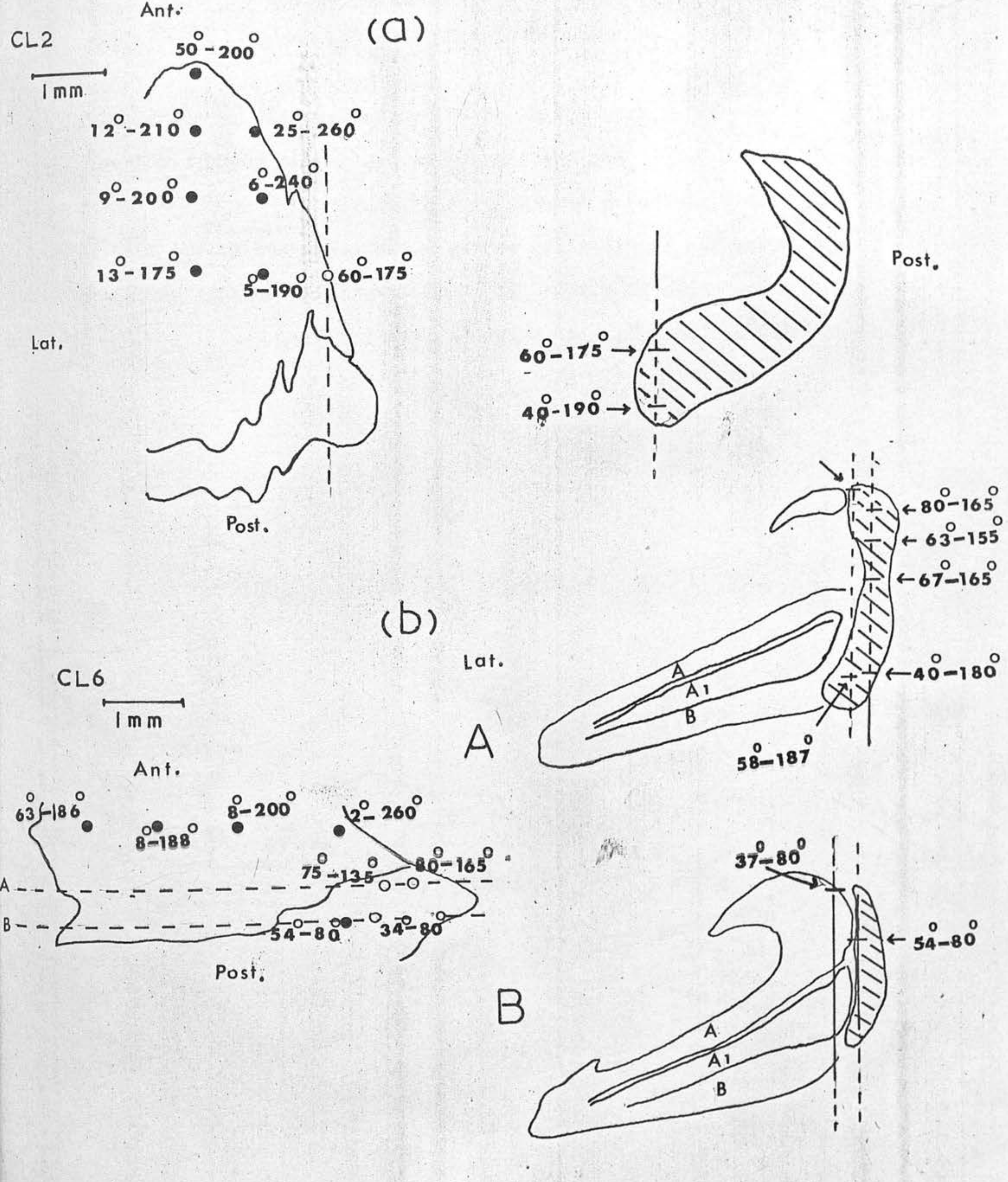
b

All the drawings of the dorsal view and the cross section of the L.G.N. in fig. 7,8,9, and 10 are on the left side of the brain and have magnification of X 15. All responses found in the left L.G.N. are in the contralateral visual field. Those mediated by the right eye are indicated by their polar co-ordinates. Those mediated by the left eye have letter 'L' after their co-ordinates.

Fig. 7

(a) On the left, part of the dorsal view of L.G.N. as reconstructed by serial sections to show the point of electrode tracks recording from the main nucleus (filled circle) and from the N.I.M. (open circle); on the right, drawing of the parasagittal section of the medial aspect of the L.G.N. passing through the N.I.M. at the level shown by broken line traversing the dorsal view of the nucleus (on the left). An electrode track is shown to penetrate the N.I.M. as indicated by vertical line (full line- electrode track as seen in the brain section, joined by imaginary broken line).Short horizontal line cutting across the electrode track is the site of recording in which the receptive field center can be localized in the visual field. (CL 2)

(b) On the left, part of the dorsal view of posterior region of the L.G.N. showing the point of entry of 3 electrode tracks passing through the N.I.M. (open circle); on the right, transverse section at 2 levels (A and B). The N.I.M. in (A) as shown by the area with diagonal lines is penetrated by 2 electrode tracks and different points of localization in the visual field are shown. (CL 6).


(a)
CL2
1mm
Ant.
50°-200°
12°-210°
25°-260°
9°-200°
6°-240°
13°-175°
5°-190°
60°-175°
Lat.
Post.
60°-175°
40°-190°
Post.
(b)
CL6
1mm
Ant.
63°-186°
8°-188°
8°-200°
2°-260°
75°-135°
80°-165°
A
B
54°-80°
34°-80°
Post.
Lat.
A
80°-165°
63°-155°
67°-165°
40°-180°
58°-187°
A
A1
B
B
37°-80°
54°-80°
A
A1
B

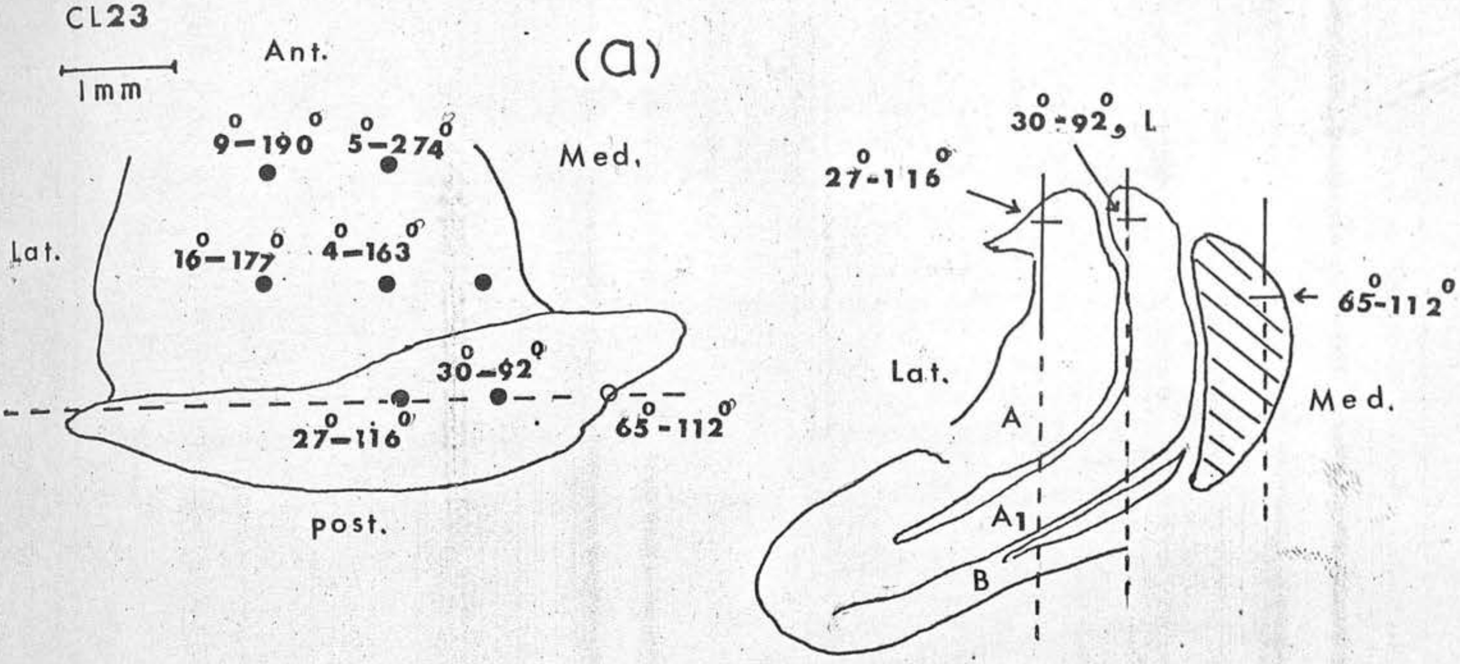
The descriptions of fig. 8,9, and 10 are the same as in fig. 7, unless otherwise indicated.

Fig. 8

(a) A dorsal view of the posterior half of the L.G.N., on the left; and the transverse section at indicated level with 3 electrode tracks, on the right.

Note; the localization of the visual response in the 2^{ry} visual area is shifted 20° - 30° from the vertical meridian, (90°), (CL 23), also shown in (b). (CL 24).

(a)


CL23
1mm
Ant.
Med.
Lat.
post.
9°-190°
5°-274°
16°-177°
4°-163°
30°-92°
27°-116°
65°-112°
30°-92°, L
27°-116°
65°-112°
Lat.
Med.
A
A1
B

(b)

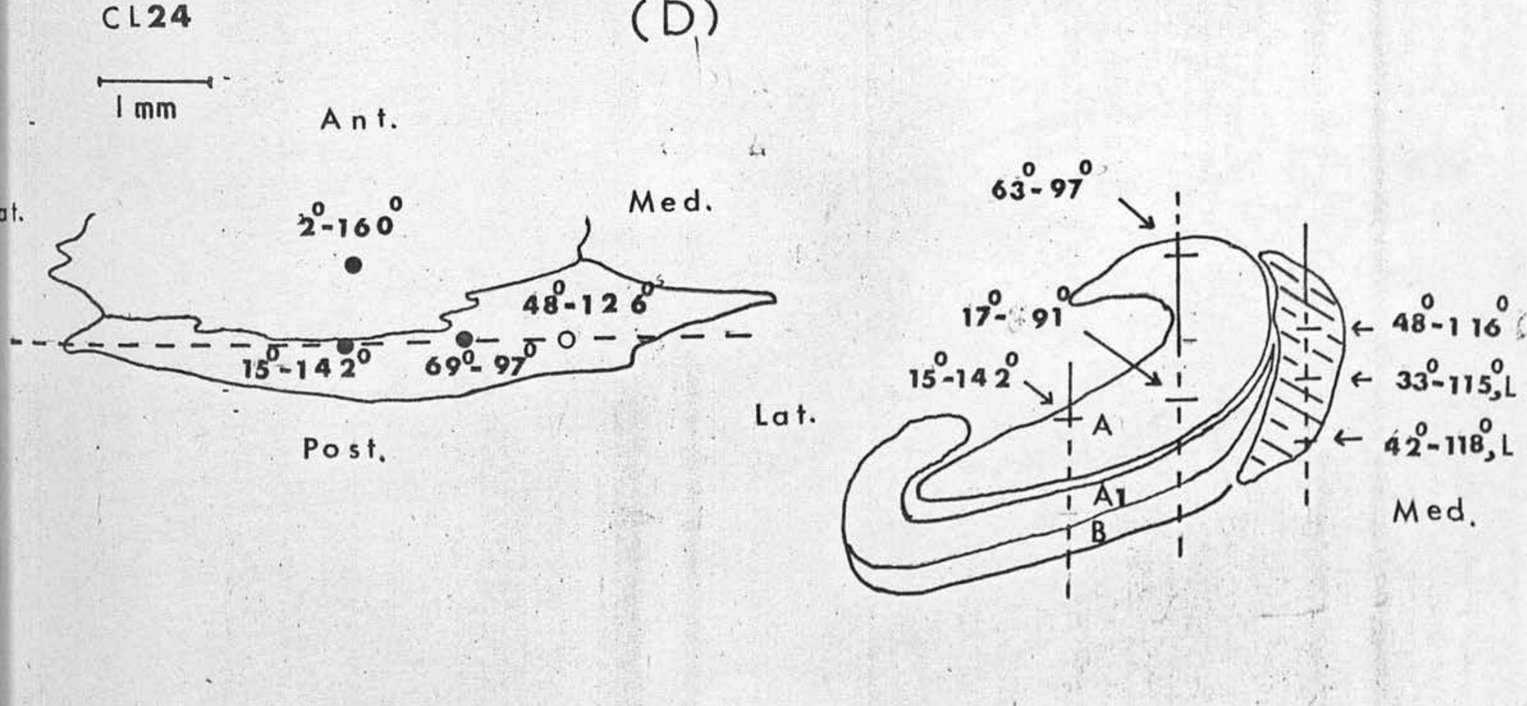

CL24
1 mm
Ant.
Med.
Post.
2°-160°
48°-126°
15°-142°
69°-97°
63°-97°
17°-91°
15°-142°
48°-116°
33°-115°, L
42°-118°, L
Lat.
Med.
A
A1
B

Fig. 9

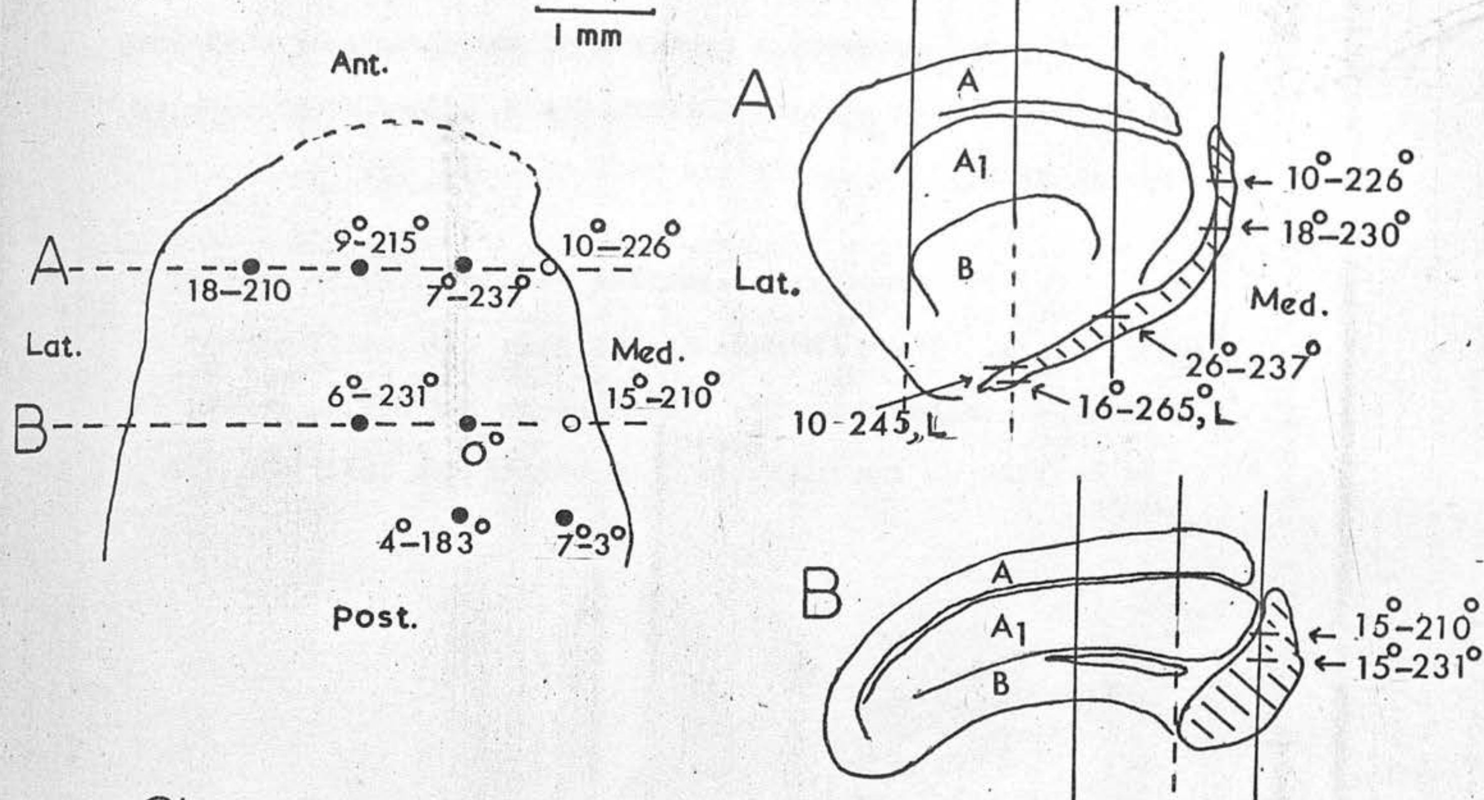
(a) On the left, a dorsal view of the anterior part of the L.G.N., with drawings of transverse section at 2 levels (A and B).

Note; all the visual responses in the 2^{ry} visual area are in the lower field. (CL 14).

(b) Another dorsal view of the L.G.N. with drawings of 2 transverse sections passing through the posterior part of the L.G.N. (CL 18).

(a)

CL14


1 mm
Ant.
A
9°-215°
10°-226°
18-210
7°-237°
Lat.
Med.
6°-231°
15°-210°
B
0°
4°-183°
7°-3°
Post.
A
A
A1
B
Lat.
Med.
10°-226°
18°-230°
26°-237°
10-245, L
16°-265°, L
B
A
A1
B
15°-210°
15°-231°

CL18

(b)

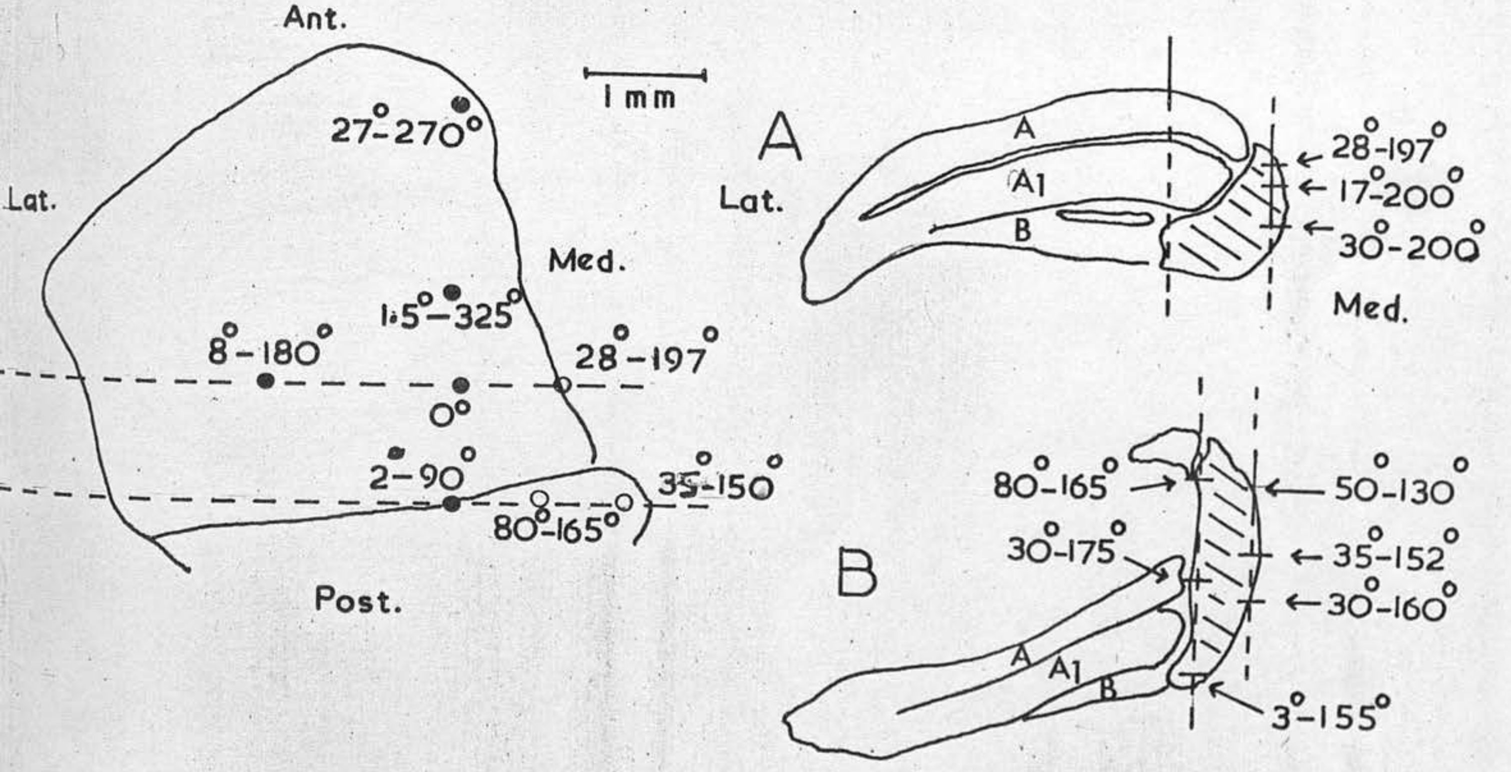

Ant.
1 mm
27°-270°
Lat.
Med.
1.5°-325°
8°-180°
28°-197°
0°
2°-90°
35°-150°
80°-165°
Post.
A
A
A1
B
Lat.
Med.
28°-197°
17°-200°
30°-200°
B
80°-165°
50°-130°
30°-175°
35°-152°
30°-160°
A
A1
B
3°-155°

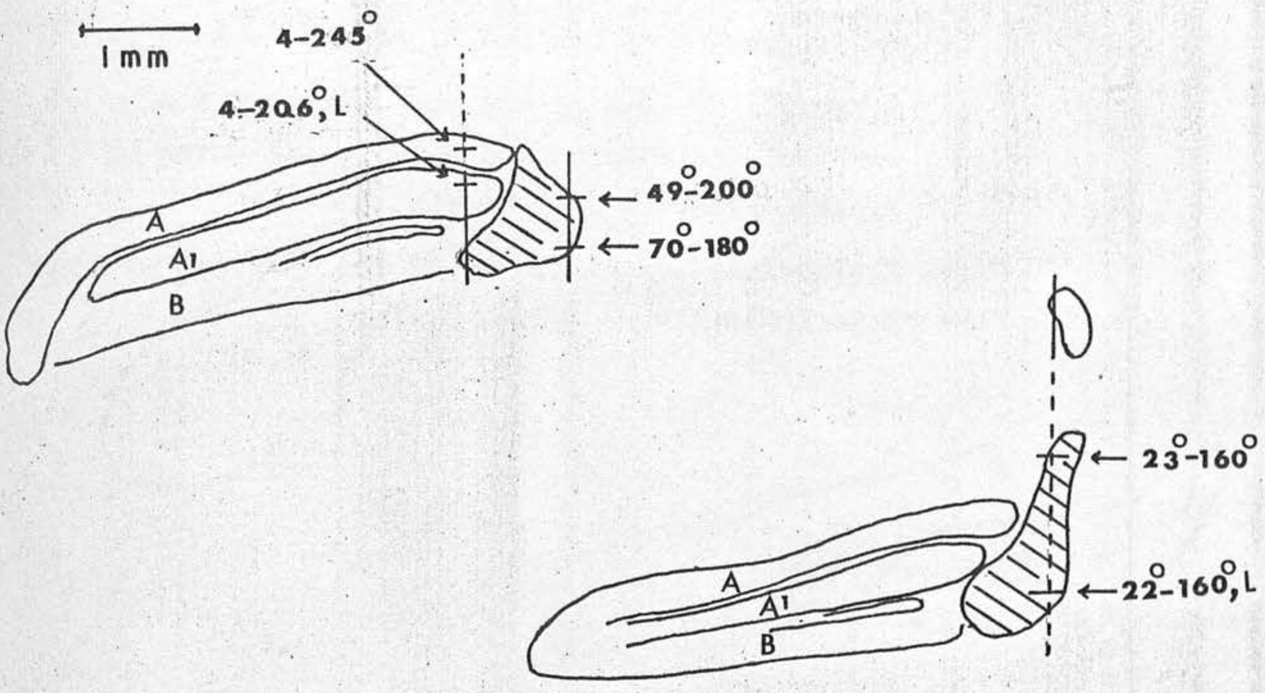
Fig. 10

(a) Two transverse sections of the L.G.N. to show the electrode tracks passing through the N.I.M.. The section on the right is 1 mm behind the left one. (CL 13)

(b) Two transverse sections at the anterior part of the L.G.N.. The electrode tracks pass the medial aspect of the main nucleus and then pass through the N.I.M. below. The section on the right is 1 mm behind the left one. (CL 35).

(a)

CL13


1 mm
4-245°
4-206°, L
49°-200°
70°-180°
A
A1
B
23°-160°
22°-160°, L
A
A1
B

CL35

(b)

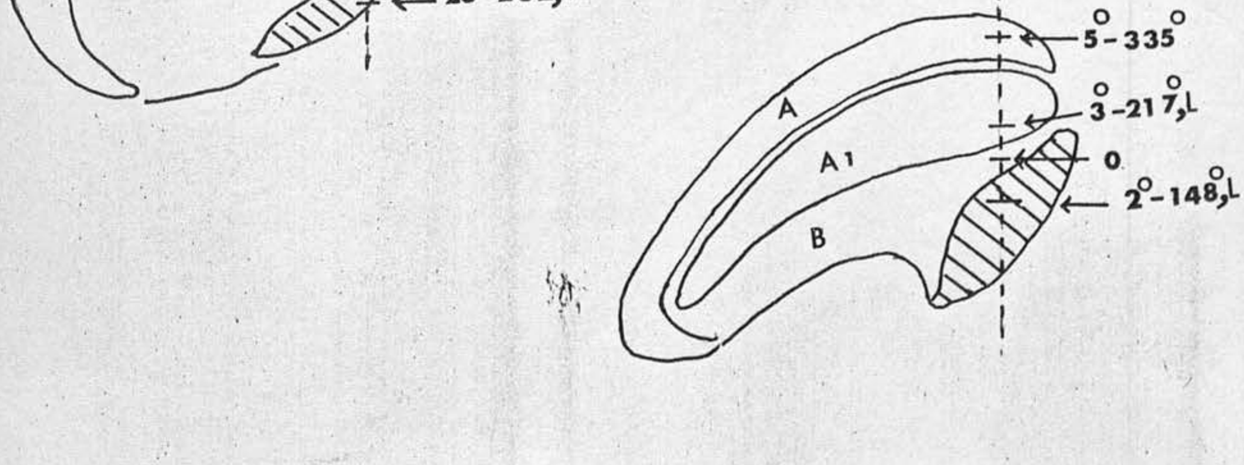

1 mm
7°-303°
6°-286°, L
28°-232°, L
A
A1
B
5°-335°
3°-217°, L
0
2°-148°, L
A
A1
B

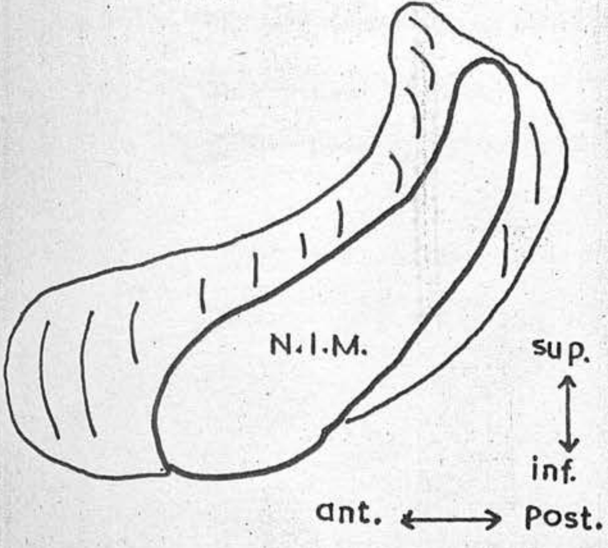
Fig. 11

Schematic diagram to show the retinotopic projection on to the N.I.M.

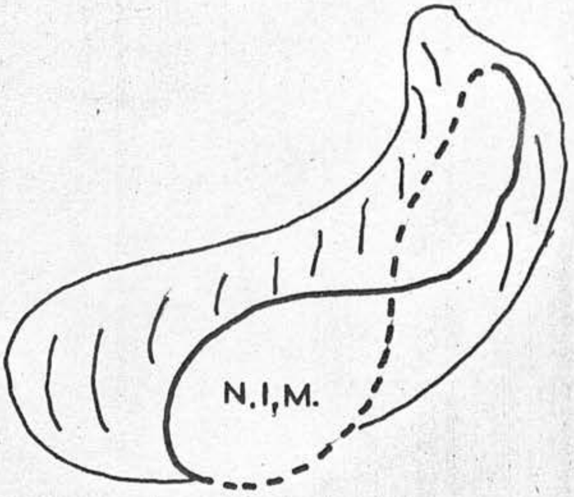
(a) Medial aspect of the L.G.N. to show the N.I.M.

(b) Schematic diagram of the projection of the vertical meridian on the N.I.M., indicated by broken lines.

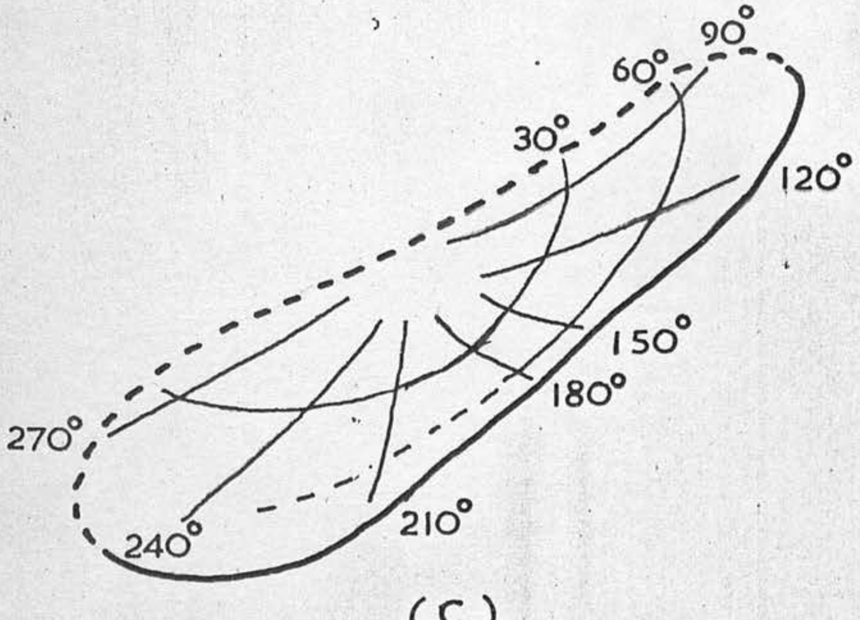
(c) Retinotopic projection on to the unfolded nucleus interlaminalis medialis.



(a)



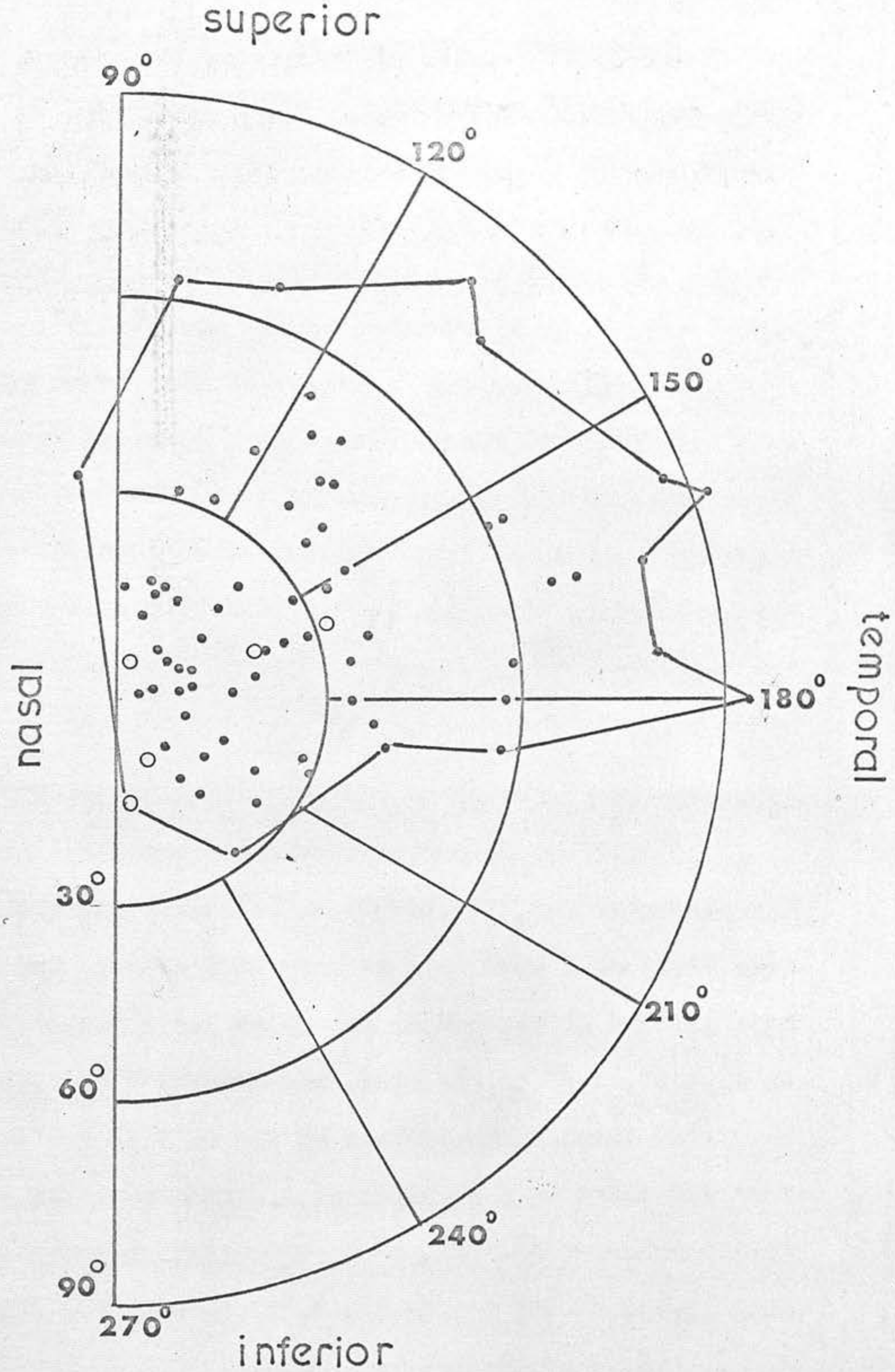
(b)



(c.)

Fig. 12

Composite results of 11 mapping experiments to illustrate the extent of the visual field subserving by the N.I.M. as plotted by physiological mapping. Filled and open circles are the points of localization in the visual field obtained from contralateral and ipsilateral eyes respectively.



Cat, visual hemi-field.

Fig. 13

(a) Response of one unit in the 2^{ry} area of the L.G.N., recorded from the N.I.M. at the postero-medial curl of the L.G.N., to 'on' and 'off' of 10 mm spot of light. For the signal of photocell in the top trace, 'on' is away from the spikes. This unit had a large receptive field about 30° across and had an approximate center at 63°-155°.

(b) - (g) show the latencies of the visual responses by a neon flash at the perimeter arm, recorded from the 2^{ry} visual area (d) to (g), comparing the latencies to the main nucleus (b) and (c). The latencies from (b) to (g) are 27.0, 26.0, 45.0, 42.0, 35.0, and 29.0 msec respectively. The arrow indicates stimulus artifact. Time in all records 100 msec. (CL6).

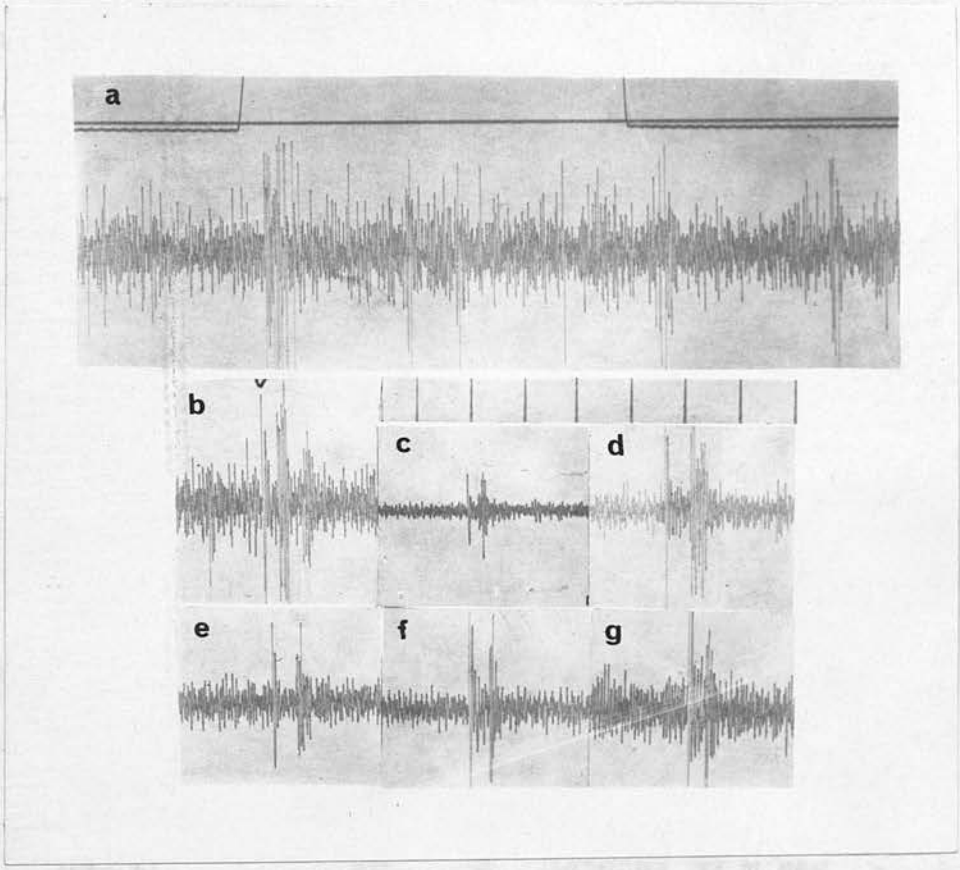
Fig. 14

(a) and (b) show latencies with neon flash placing at the perimeter arm, to the N.I.M. (a) which had the receptive field on 2°-148° and latency 28.5 m sec; and to the main nucleus of the L.G.N. (b) which had a receptive field on 6°-125°, 1.5° in diameter, and latency 28.0 m sec.

(c) shows the responses of the unit in the N.I.M. to 'on' and 'off' of 5 mm light spot. This unit had a receptive field center at 28-232°, 5° in diameter. For the photocell signal in the top trace, 'off' is away from the spikes.

Time in all records 10 m sec.

13



14

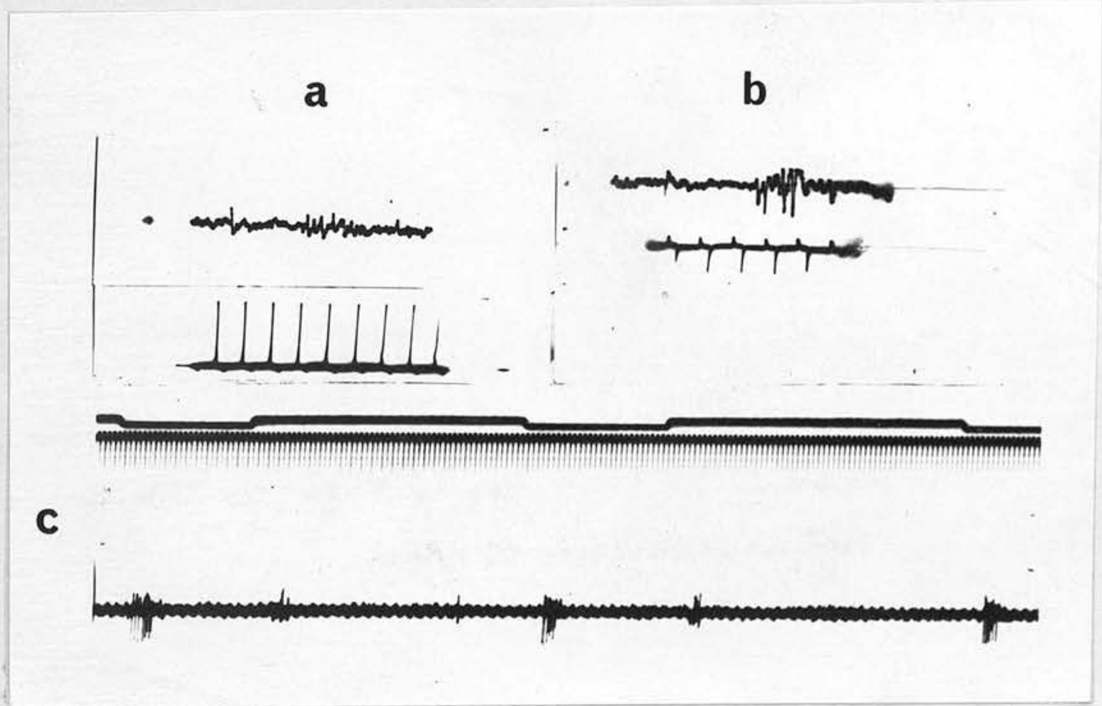


Table 1: Single units recorded from the N.I.M.

No.	Expt.	position	receptive field size	eye	characteristics
1	CL 5	45°-180°	about 60° across	R	latency 40 m/sec.
2	CL 6	63-155	5°	L	'on' center, latency 25 m/sec.
3	"	26-215	20°	R	
4	CL12	17-170	15°	R	
5	"	17-200	—	R	'off' center, prolonged after discharge
6	"	30-200	—	R	'on' center
7	"	18-230	20°	R	latency 30 m/sec
8	"	3-155	—	R	'on' center, prolonged after discharge
9	"	35-152	10°	R	'on' center
10	"	30-160	—	R	'on' center
11	"	80-175	10°	R	'on' center
12	CL35	28-232	5°	L	'on' center, latency 25 m/sec
13	CL23	65-112	8°	R	

(R = right eye, L = left eye)

THE SUPERIOR COLLICULUS OF THE CAT

II. THE SUPERIOR COLLICULUS OF THE CAT

Twenty-eight cats were used in the experiments on the S.C., 7 in the mapping experiments, 13 in the single unit studies, and 8 in the cooling experiments as well as single unit studies.

A. THE RETINAL REPRESENTATION ON THE SUPERIOR COLLICULUS

1. Anatomical observations

The main task was to determine the retinotopic organization onto the surface of the S.C.. In order to do this, it was necessary to define the boundary of the S.C. and it was decided to use the extent of the superficial cell layer, stratum griseum superficiale, as a boundary of the S.C..

In the course of this study, some anatomical observations have been added. In the toluidine blue stained sections, the layers of the superior colliculus are fairly clearly defined in the upper part but not in the lower part. The stratum griseum superficiale has greatest thickness in the central region, being about 0.6 to 0.8 mm., and thins out progressively as it reaches the peripheral part. The thickness of the stratum opticum is about 0.7-1.0 mm. in the central part. The adjacent deeper layer, stratum griseum intermediale, has about the same thickness as the stratum opticum, but in some histological sections, it was found that the boundary between the two layers could only be determined approximately (Fig. 15).

The surface of the S.C. is curved in the medio-lateral as well as antero-posterior plane, especially the extreme lateral part. It was therdfore necessary to transform this surface into a flat surface for accuracy in mapping experiments. The surface of the left S.C. of 5 cats were flattened out as explained in the section on experimental methods, and the surface areas were calculated. The average value obtained was 33 mm^2. (Table 2).

2. The retinotopic projection onto the superior colliculus

The projection of the visual field was determined in 5 experiments, from which the results are reproduced - Experiments CS2 Figure 16, Experiment CS4 Figure 17, Experiment CS1 Figure 18, Experiment CS20 Figure 19, and Experiment CS5 Figure 20.

The positions of maximal response in the right visual field are shown corresponding with the positions of the electrode on the surface of the left S.C.. Each point in the right visual field is represented by a point in the S.C., so that the horizontal and vertical dimensions of the cat's visual field are projected as a two-dimensional map onto the surface of the contralateral S.C., The point of localization in the visual field was made when the electrode was in the very superficial part of the S.C., because the receptive field is smallest here; by passing the electrode through the S.C. and recording from different depths, it was found that the receptive field became larger and larger, and thus the center of the receptive field could not be determined with certainty.

The general outline of these results establishes clearly that the central visual field is represented on the anterior part of the S.C. with the peripheral field posteriorly. The upper field quadrant is projected onto the antero-medial part of the S.C. while the lower field quadrant is represented on to the postero-lateral part. The projections of the meridians of the visual field radiate backward and medially; the upper vertical meridian (0°-90°) runs medially along the anterior border of the S.C., the lower vertical meridian (0°-270°) laterally along the anterior edge of the S.C., and the horizontal meridian (0°-180°) runs backwards and medially.

The dorsal view projections are also produced in the Figures 16, 17, and 18 to show the differences of the shape and retinotopic patterns of the S.C. before and after flattening out.

The central field is represented on a disproportionately large extent of the collicular surface, compared with the peripheral field. The area of the surface enclosed by the

10° semicircle occupies almost one-fourth of the available surface, while the 30° semi-circle, almost half, and correspondingly the smaller area in the more peripheral field. The surface areas of the S.C. subserving different semi-circles in the visual field are shown in Table 3 in detail.

The results also establish that the horizontal meridian (0°-180°) divides the collicular surface into 2 halves, the medial part for the upper visual field and the lateral part for the lower visual field. The areas devoted to the upper field and lower field quadrants show significant difference. The average surface areas of the upper and lower field quadrants, as measured from 5 experiments, are 42 % and 58 % respectively (Table 2).

Equal sectors of the visual field do not correspond to equal areas on the S.C.; the sectors adjacent to the horizontal meridian enclose between them the greater part of the surface of the S.C., while the sectors near the vertical meridian take up a smaller area. This is clearly illustrated in Table 3.

3. The magnification factor along the horizontal meridian

The variations of the magnification factor with retinal eccentricity along the horizontal meridian were determined and the composite results of 5 experiments are reproduced. (Fig. 21).

The magnification factors along a horizontal meridian are maximal at the center (mean 0.9 mm./degree) falling off rapidly to a mean value of 0.1 mm./degree at 10° out from the center of fixation and after that falling gradually to a mean value of 0.02 mm./degree at 60° from the fixation point.

In order to compare the magnification factors along a horizontal meridian for different visual centers, the results of the magnification factors of the L.G.N. as reproduced from Seneviratne (1963), and centroperipheral ganglion cell density of the retina (Stone, 1965), are plotted together against the retinal eccentricity. (Fig. 22). In general, all 3 curves show approximately the same pattern, with minor differences. They fall off within 10° from the fixation point and after that fall gradually. The pattern of ganglion cell distribution in the retina is similar to the variations of a magnification factor with retinal eccentricity.

4. The extent of the visual field

All peripheral limits of the visual field have not been obtained during the course of any single experiment, so it was necessary to combine all the experiments as the composite result (Fig. 23). The results show that the localizations have been obtained, 35° above and 45° below the fixation point on the vertical meridian, and 85° temporal to the fixation point on the plane surface projection of the S.C.; it is evident that some small areas of the collicularsurface peripheral to these values, have not been studied in the region of a horizontal meridian. Thus it is likely that the horizontal meridian is represented up to 90°, but the upper and lower visual fields seem to have restricted representation, and particularly the upper field.

5. The representation of the area centralis

The present experiments have described the projection of the area centralis onto the anterior edge of the S.C.. On a few occasions the localizations were exactly on the center of fixation, and the area of the superior colliculus subserving the central area within 2° occupies about 10% of the total surface, as measured in 2 experiments. These findings are in agreement with the anatomical studies of Laties and Sprague (1966) who made lesions in the area centralis, and by Nauta-Laidlaw technique found degeneration bilaterally in the rostral one-third to one-fourth of the S.C., this being considerably heavier on the crossed side.

B. SINGLE UNIT ACTIVITY OF THE SUPERIOR COLLICULUS

The recording site in the S.C. has been determined by two methods; first, by using electrolytic lesions and, secondly, by observing the position where the electrode first touches surface of the S.C. An electrolytic lesion was made at the site of the unit recorded, usually only one lesion at one penetration. The sites of recordings at different depths can be measured from the drawing of the enlarged histological sections. The point of an electrode touching the collicular surface was found to be a characteristic feature. When an electrode is above the colliculus it is possible to record diphasic responses from the stimulation of a neon flash at the eye or at the localizing point at the perimeter arm. When the electrode contacts the surface of the S.C. the diphasic slow wave suddenly increases in amplitude and a sharp crackle of the axon and cell action potentials is heard or seen in the oscilloscope. The estimation of the point from which a given unit is recorded by referring the depth reading to that of the collicular surface as read when the electrode is touching the S.C., was found to be fairly accurate.

General features of units recorded from the superior colliculus

After the electrode has just touched the collicular surface, the units with "small receptive field" (1°-3° in diameter) are invariably recorded. When the electrode travels down deeper and deeper the receptive field becomes bigger and bigger, becoming "medium-sized field" (3°-10° in diameter), or "large receptive field" (over 10° to about 40° in diameter.).

The optimum stimulus for these units is a moving object. The small receptive field requires very slow movement, about 0.5°-1.0°/sec., the medium-sized receptive field, moderate movement, about 5°-40°/sec., and the large receptive field, 100°-300°/sec. Generally speaking, the velocity increases with the size of the receptive field.

As the electrode is passing down, at a certain depth, about 0.6-0.8 mm. from the surface, it will be found that a hissing sound like that of many fibers firing can be heard. This depth corresponds to the transitional zone between the stratum griseum superficiale and the stratum opticum. Spontaneous firing units can be isolated occasionally against fiber background. Besides some large field units, two types of unit are found, namely, "directionally selective unit", and "specific orientation unit". The optimum stimulus for the former is the movement in a particular direction and, for the latter, is a movement of a straight boundary with a particular orientation. When the electrode enters the stratum griseum intermediale, as verified by an electrolytic lesion, the usual fiber background disappears. Some spontaneous firing units are found, the majority of them being non-visual. Visual units recorded from this layer show new characteristics. They respond only to fast movement in one direction and show no response at all in other directions. The various kinds of unit described above will be considered in detail below.

CLASSIFICATION OF UNITS RECORDED IN THE SUPERIOR COLLICULUS

In the course of the experiments, 150 units have been studied. These units responded differently to visual stimuli, as briefly described above, and can be classified into 5 groups (Table 4). The behaviour of these units is illustrated in Fig. 25 and the histogram showing the distribution of units in different layers is shown in Fig. 24.

1. Small receptive field unit

The receptive fieldsof 51 of the 150 collicular units in this series were classified as "small receptive field unit". The main features of this class of units are: (1) The responses occur only to slow movements of a stimulus, and (2) Vigorous responses are obtained only with a small stimulus.

The diameters of their field are small, ranging from $1/2^{o}$ to 3^{o} in diameter (mean diameter 2^{o}). The small receptive field units recorded from the different parts of the S.C. have been observed, and their positions were distributed in different sectors of the visual field, being situated up to 60^{o} from the fixation point along the horizontal meridian. The relationship between the size of the receptive field and eccentricity have also been observed, and it is found that the size of a receptive field increases very little, or remains within the same range as the locations proceed from the central to peripheral field. A few units have been observed 60° out from the fixation point and still had receptive fields 2°-3° in diameter.

The optimum stimulus for this kind of unit was a slow moving stimulus. Usually the speed of movement which elicited the response was as slow as 0.5°-2.0°/sec., and there was frequently little or no response at all for movements faster than 10°/sec. The optimum speed was 0.5°-2.0°/sec. (Fig. 26c).

This type of unit shows lateral inhibition, as demonstrated by a stimulus bigger than the receptive field moving across the receptive field. The responses become weaker and weaker as bigger and bigger stimuli are used. No response could be elicited by turning a spot of light on or off in the receptive field or the periphery. Most of the units in this group were obtained from the upper part of the stratum griseum superficiale, about half of them were recorded from just under the surface of the superior colliculus.

Since none of the units has been found to fire spontaneously under chloralose anaesthesia, and their small receptive field responded only to very slow movement of an optimum size of stimulus, it was difficult to know at first whether or not such a unit was recorded by the electrode. The technique of localizing the receptive field by a neon flash when the electrode had touched the collicular surface was found to be a useful guide in finding an approximate position of the receptive field.

2. Medium sized receptive field unit

Units in this group had medium-sized receptive fields and responded to a moderate rate of movement. Thirty-four units fell in this class, and consisted of 22.67% of the total sample. Twenty-eight units were recorded from the stratum griseum superficiale, almost half of them were in the upper part and the other half in the lower part; only 6 units were found in the stratum opticum. Among the units in the upper part of the stratum griseum superficiale, most of them were obtained below the small receptive field units.

The size of a receptive field varied from 3° to 10° in diameter; in general, the receptive fields recorded from the upper part are smaller than in the lower part. The optimum stimulus was a contrasting edge moving across the receptive field at a velocity of 5° to 40°/sec. (Fig. 26 e). No preferential direction was detected. Some, but not all, of these units respond to 'on' and 'off' of the perimeter spot everywhere in the receptive field. (Fig. 26 d). The medium-sized receptive field units differ from the small receptive field in that more than half of them showed spontaneous activity under light chloralose anaesthesia.

3. Large receptive field unit

The main characteristics of this kind of unit are a large receptive field and response to fast movement without a preferential direction. Thirty-two units were observed in this series which consisted of 21.33% of the total. The majority of them, 22 units, were found in both upper and lower halves of the stratum opticum, only some 6 units were recorded from the lower part of the stratum griseum superficiale.

Under light chloralose anaesthesia units of this type showed high levels of spontaneous activity. The optimum stimulus was a movement of high velocity across the receptive field in any direction. No preferential directions were detected. The optimum rate varied from unit to unit but was within the range 70°-300°/sec. In Fig. 27, the responses of a large receptive field unit are shown; (a) shows the response to a light spot turned on and off, and (b) and (c) show responses to fast movement. Though the majority of the units of this kind were recorded from the fiber layer (stratum opticum), the action potentials of the units encountered were more characteristic of cells; showing notches on the ascending limb and a long duration.

The receptive field areas varied from over 10° to about 40° in diameter. The shape of the receptive field was more or less circular or oval. Some fields were found to have an oval shape with their long axis along the horizontal meridian. Most of the units, however, had the receptive field center in the sectors around the horizontal meridian.

4. Specific orientation unit

The special feature of this class of unit is that the response occurs only to a movement of a contrasting straight edge with a particular orientation. Among the 12 units which consisted of 8.0% of the total, 9 units were recorded from the stratum opticum (4 in the upper half and 5 in the lower half) only 3 of them were obtained in the lower part of the stratum griseum superficiale.

All units in this category respond either to a slit of light moving across the receptive field in a particular orientation or black-card-board bar moving against a white background. Tilting of the stimulus about 45° from the preferred orientation was usually enough to reduce a response greatly,or even abolished it. (Fig. 28 A,B). It seemed that these subgroups correspond to the simple and complex receptive fields in the cat's visual cortex respectively (Hubel and Wiesel, 1962). Since most of these cells gave little or no response to stationary patterns, the distribution of their excitatory and inhibitory regions is not known with certainty.

5. Directionally selective unit

This group of 24 units, consisting of 14.0% of the total, could be stimulated only to a movement in one direction, but not in the opposite direction. The locations from which these units were recorded were in the stratum opticum and the stratum griseum intermediale in the majority of cases; only 4 units were found in the lower part of the stratum griseum superficiale.

In the early part of the experiments, directionally selective units were found as deep as the lower part of the stratum opticum (11 units). These directional units require moderate movements as an optimum stimulus. In Fig. 26 b, the responses of a directionally selective unit to a rectangular light bar moving back and forth across the receptive field with an approximate velocity of 30°/sec. are shown. In this case some responses could be elicited in the direction opposite to the best direction but these were much weaker. Various preferred directions have been observed including a centripetal direction (3 units), a movement from the peripheral field into the fixation point; centrifugal direction (2 units), moving away from the fixation point; as well as the other directions (6 units).

It was a the later stage that the directionally selective units in the deeper layer (stratum griseum intermediale) were discovered. These units responded only to fast movement in a centrifugal direction within a certain range. (Fig.29, 30).

The most striking property of this kind of unit was the response to movement in a centrifugal direction and the absence of any response at all for movement in other directions. The optimum velocities observed were in the range of 100°-300°/ /sec. The responses obtained consisted of a brief discharge of only a few spikes.

Size of action potentials

Though the amplitude of the action potential was not routinely measured, in general, those from the small receptive field unit was of very small size (about 50-100 uv); whilst those from a large receptive field unit, directionally selective unit, and a specific orientation unit, were of medium and large sizes. (up to millivolts in some units).

C. INFLUENCE OF THE VISUAL CORTEX UPON THE UNIT ACTIVITY IN THE SUPERIOR COLLICULUS

This series of experiments began when the single units with complex receptive fields had been discovered in the S.C.. Some of these units behaved in a way similar to or related to the units described in the cat's visual cortex by Hubel and Wiesel (1959, 1962). Moreover, projections from the visual cortex to the S.C. have been repeatedly demonstrated by anatomical methods (Barris et al, 1935; Béresford, 1961; Altman, 1962; and Sprague, 1963), as well as by electrophysiological methods using strychnine neuronography (Niemer and Jimenez-Castellanos, 1950; and Jassik-Gerschenfeld, 1963). It was, therefore, thought necessary to determine how far the properties of units in the superior colliculus are dependent on the cortical function.

Over all 18 units have, so far, been studied by cooling the corresponding part of the visual cortex (visual I), and studying the activity of the units recorded from the S.C.. 7 units were found to be changed in their activity. The positions of the units studied are shown in Fig. 32.

Units with changed behaviour

The majority of units which were changed in activity by cooling was in the stratum opticum (3 in the upper half, and 2 in the lower half); 2 units were in the upper part of the stratum griseum intermediale. None were found in the superficial cell layer. (stratum griseum superficiale).

Four units had large receptive fields. 2 to 5 min. after cooling had been applied to the visual cortex, these units no longer responded to visual stimuli as shown in Fig. 31 (d) and (e). Of the two spontaneously firing units which have been observed, one of them lost its spontaneous activity as well as the visual responses when cooling had been applied. Another spontaneously active unit retained spontaneous activity but could not be excited by visual stimuli.

In one medium-sized receptive field unit, the visual responses and spontaneous activity disappeared during cooling of the visual cortex.

Two units showed the characteristics of the 'simple' subgroup of specific orientation unit. Both units fired spontaneously and one of them showed no responses to visual stimuli as well as cessation of spontaneous activity after the corresponding part of the visual cortex had been cooled. Another unit still showed spontaneous activity in spite of the loss of the visual response by cooling. (Fig. 31, a,b,c.).

One to five minutes after the blockage of the visual cortex had been removed, all collicular responses to visual stimuli of the units described above could be obtained again. Some of them were cooled twice and the same results were obtained.

Unaffected units

Of 12 units in this group, half of them (6 units) were in the group of small receptive field units, and were recorded from the upper part of the stratum griseum superficiale. The other unchanged units were:- 3 large receptive field units, 2 medium-sized receptive field units, and 1 directionally selective unit. The activity of these units was unaltered by cooling applied up to 8 or 10 minutes.

Fig. 15

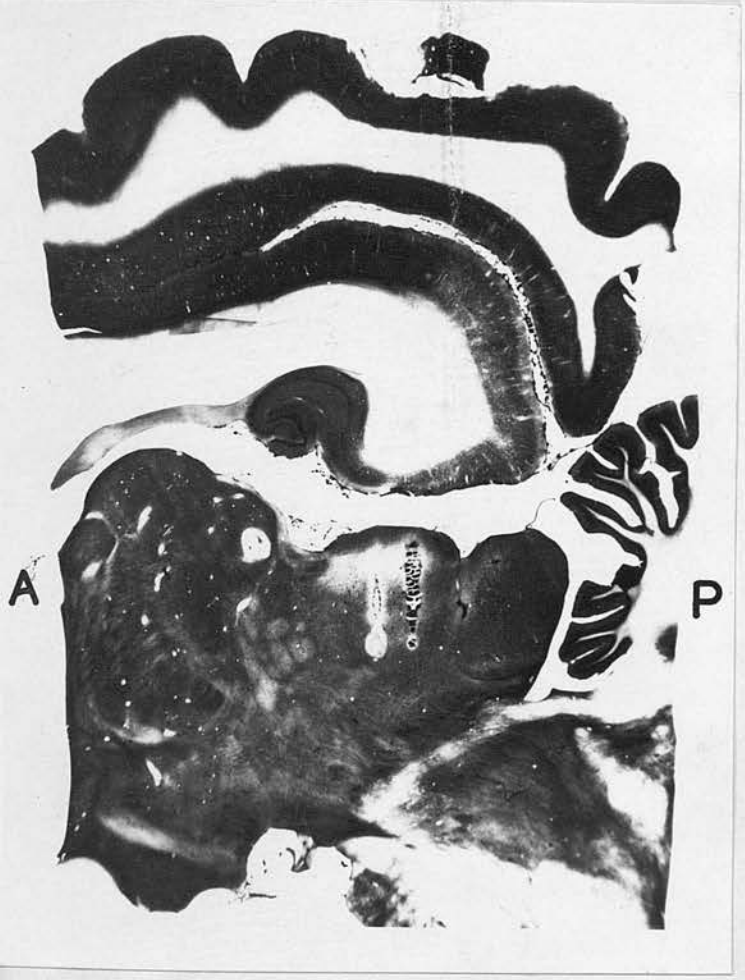
(a) A parasagittal section of cat's brain to show the superior colliculus with two electrode tracks passing through.

Section magnification X 4.

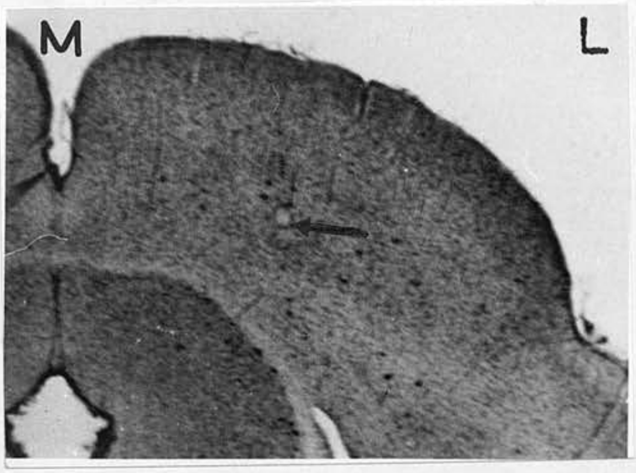
(b) and (c) Photomicrograph of transverse section of cat's superior colliculus to show the electrolytic lesions, indicated by arrows. Lesion in (b) is in the middle part of the stratum griseum intermediale and in the lower part in (c). (b.- CS27, c.- CS 8)

Section magnification X 13 in (b) and X 12 in (c).

a



b



c

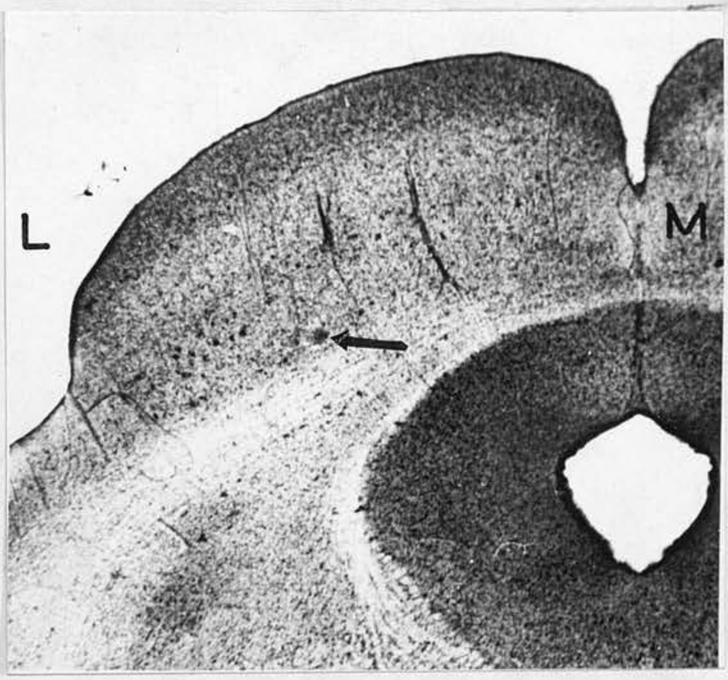
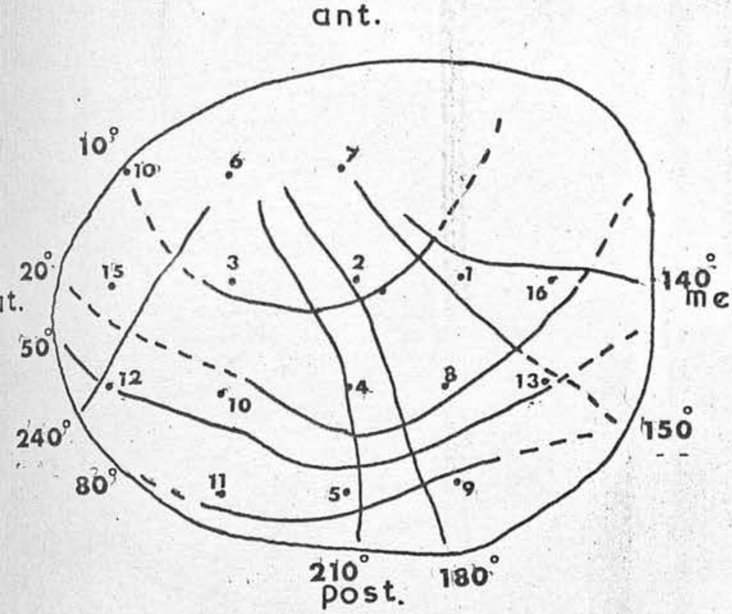
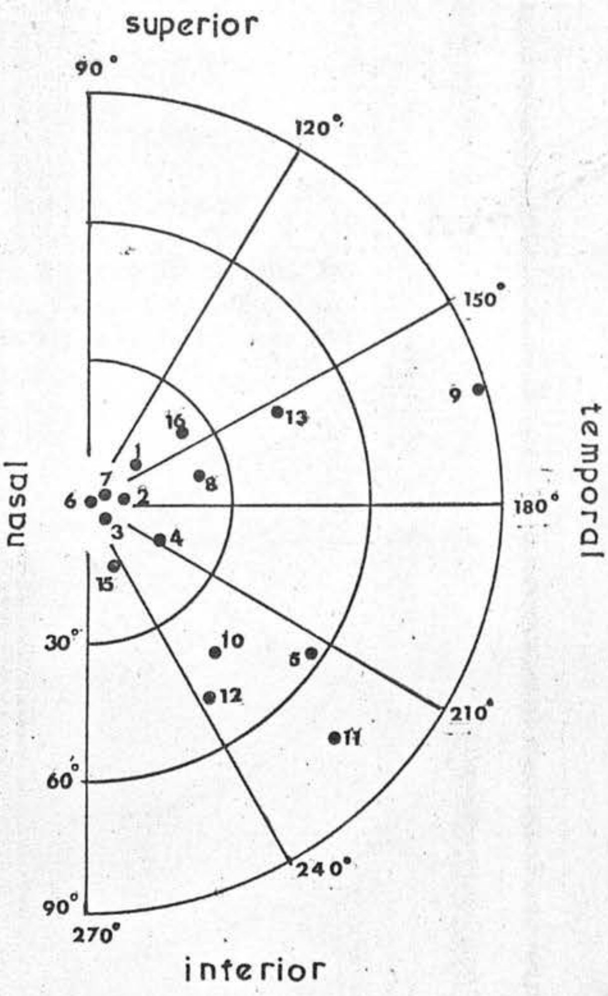


Fig. 16

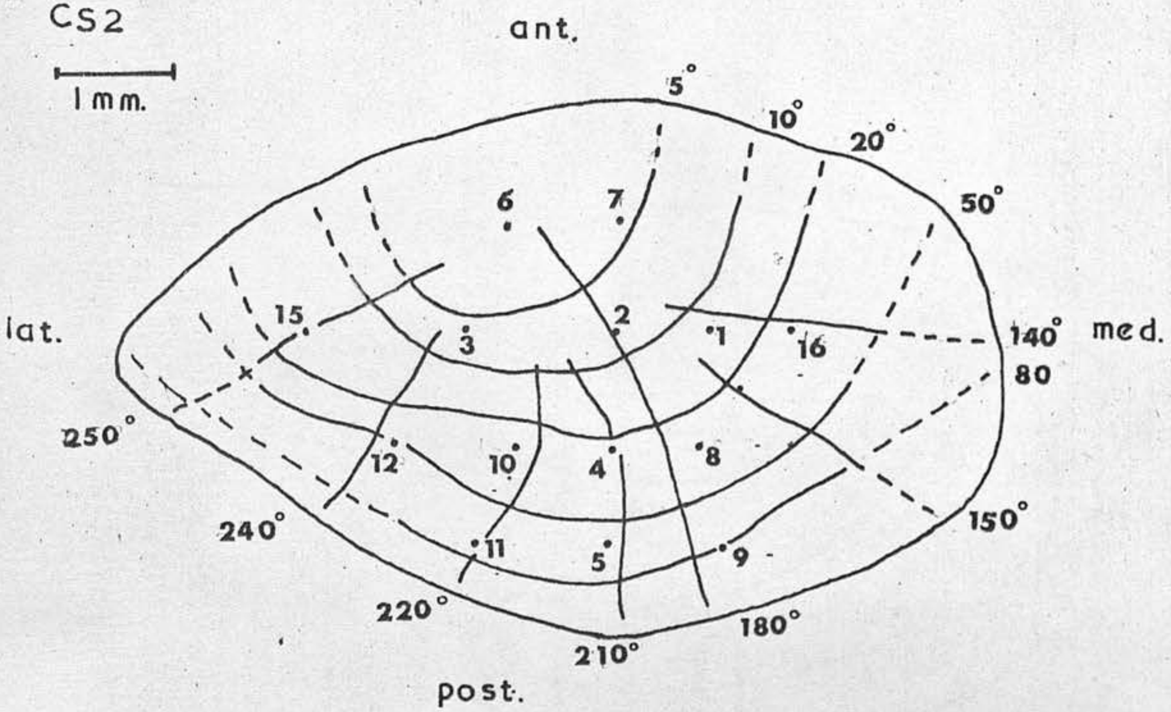
Projection of the visual hemi-field of the right eye on the left dorsal surface of the cat's superior colliculus, dorsal view and plane projections (CS2).



Dorsal view projection.



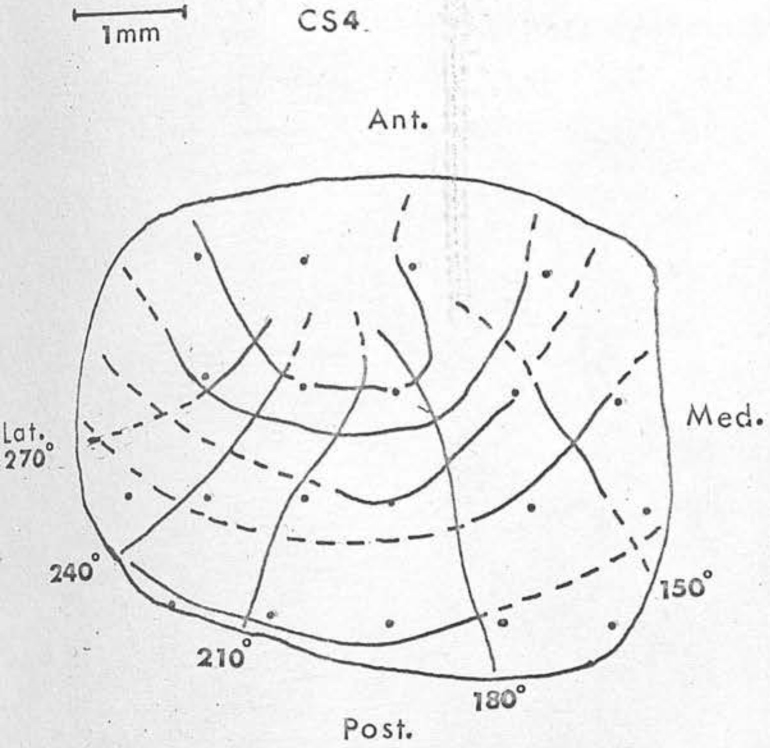
Cat. visual hemi-field, right eye.



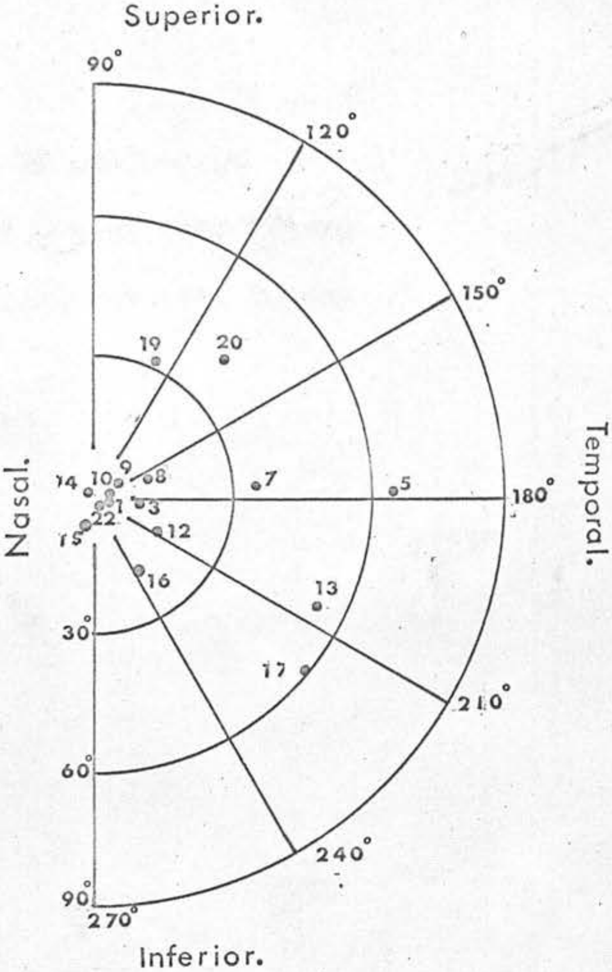
Plane projection of surface of superior colliculus, left.

Fig. 17

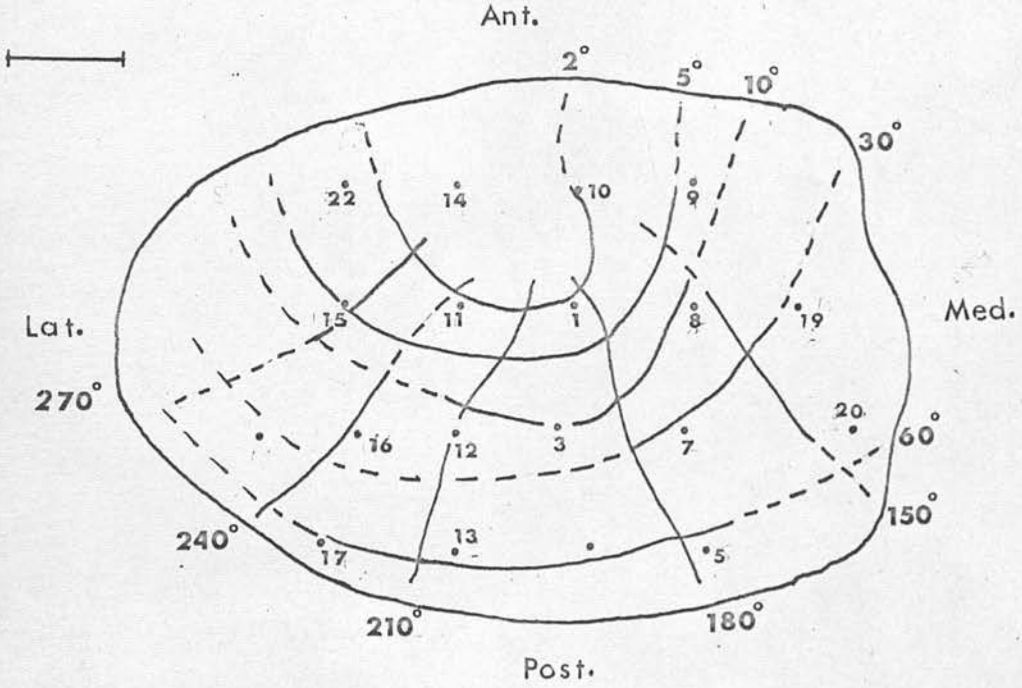
Projection of the visual hemi-field of the right eye on the left dorsal surface of the cat's superior colliculus, dorsal view and plane projections (CS 4)



DORSAL VIEW, SUPERIOR COLLICULUS, LEFT.



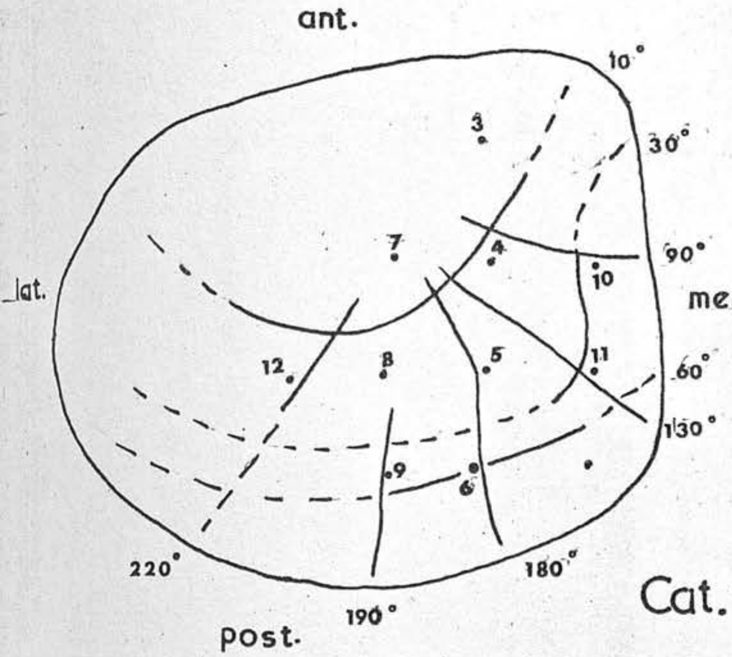
CAT. VISUAL HEMI FIELD, RIGHT EYE.



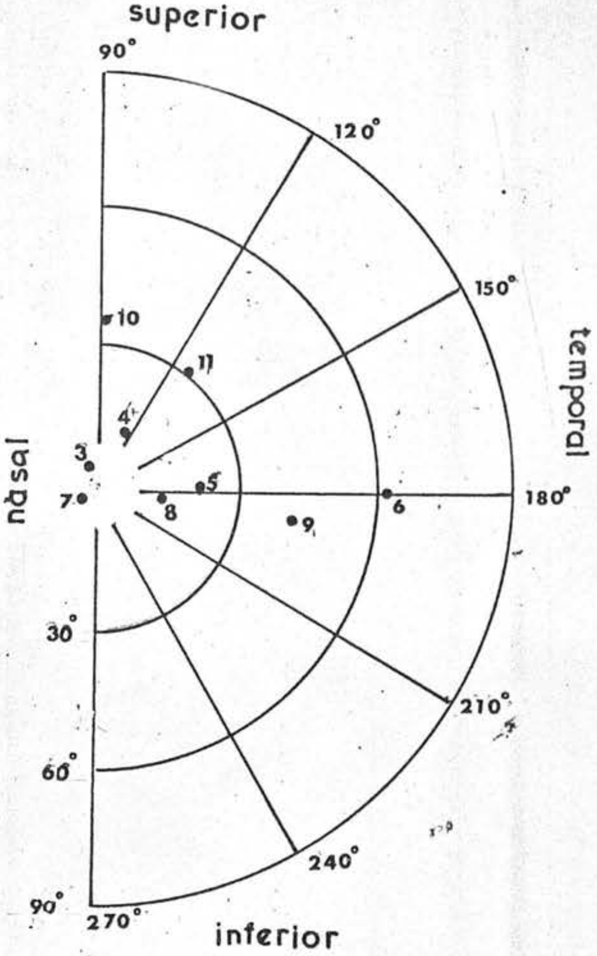
PLANE PROJECTION OF SURFACE OF SUPERIOR COLLICULUS, LEFT.

Fig. 18

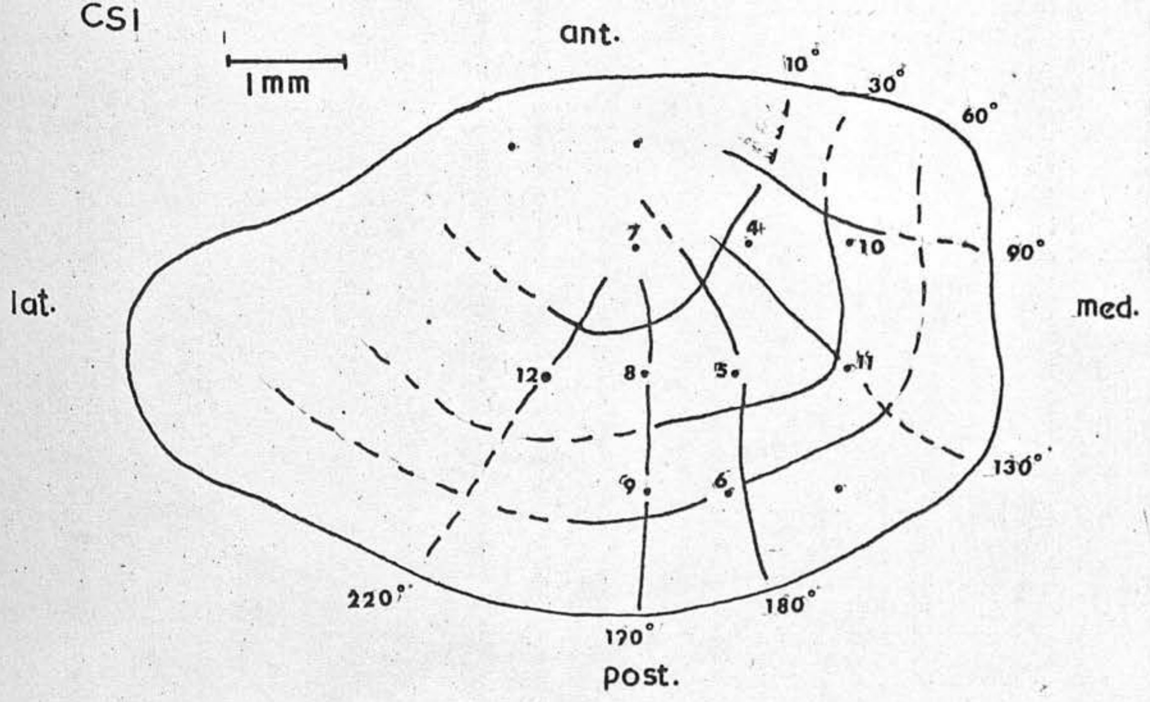
Projection of the visual hemi-field of the right eye on the left dorsal surface of the cat's superior colliculus, dorsal view and plane projections (CS1).



Dorsal view projection.



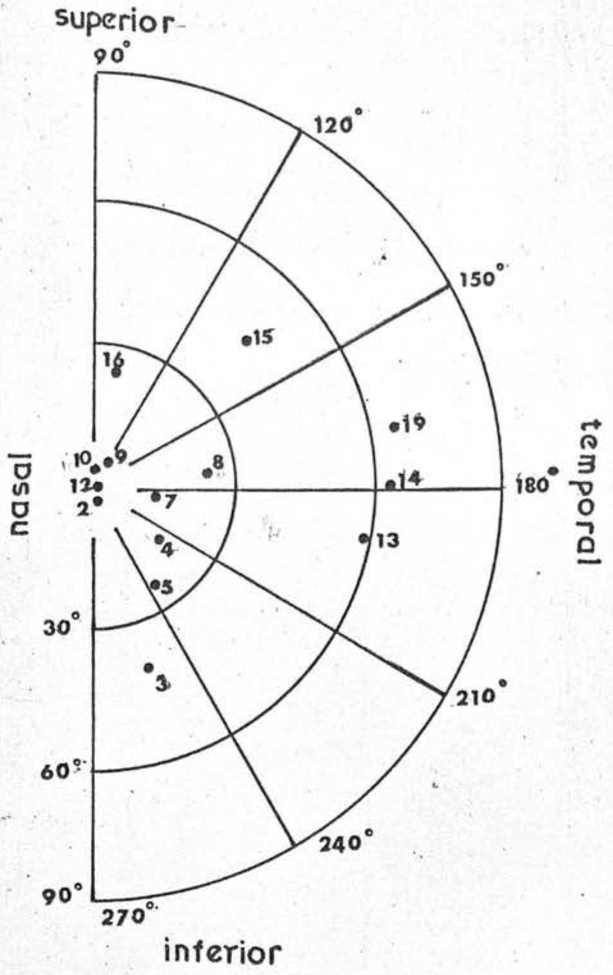
Cat. visual hemi-field, right eye.



Plane projection of surface of superior colliculus, left.

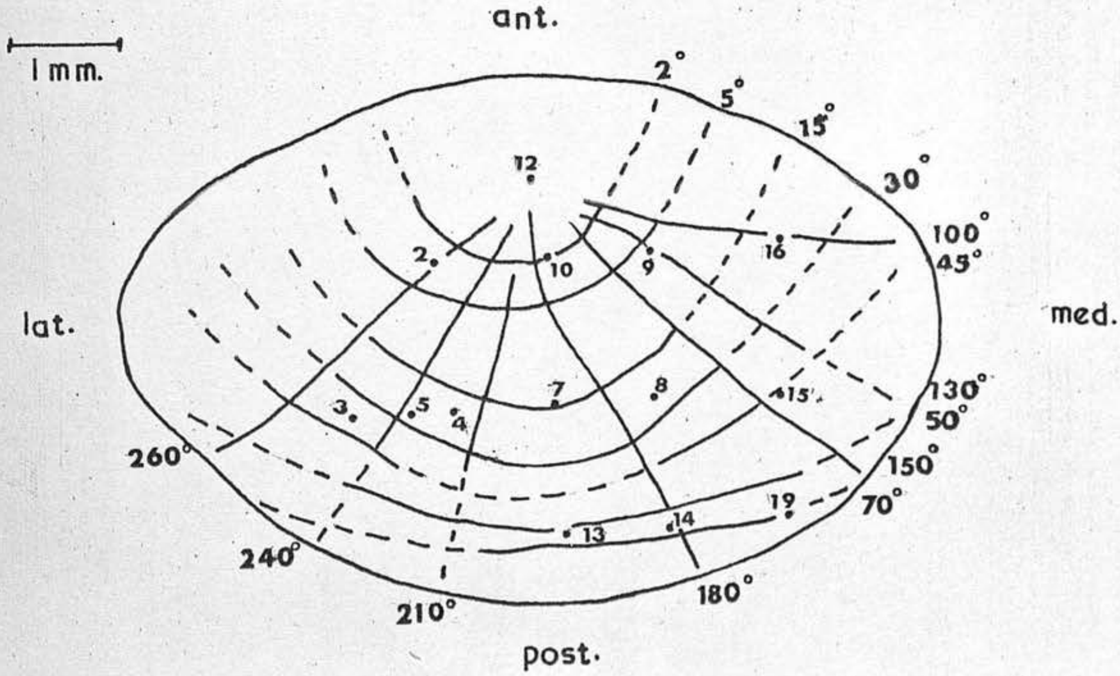
Fig. 19

Projection of the visual hemi-field of the right eye on the left dorsal surface of the cat's superior colliculus, plane projection (CS20).



Cat, visual hemi-field right eye.

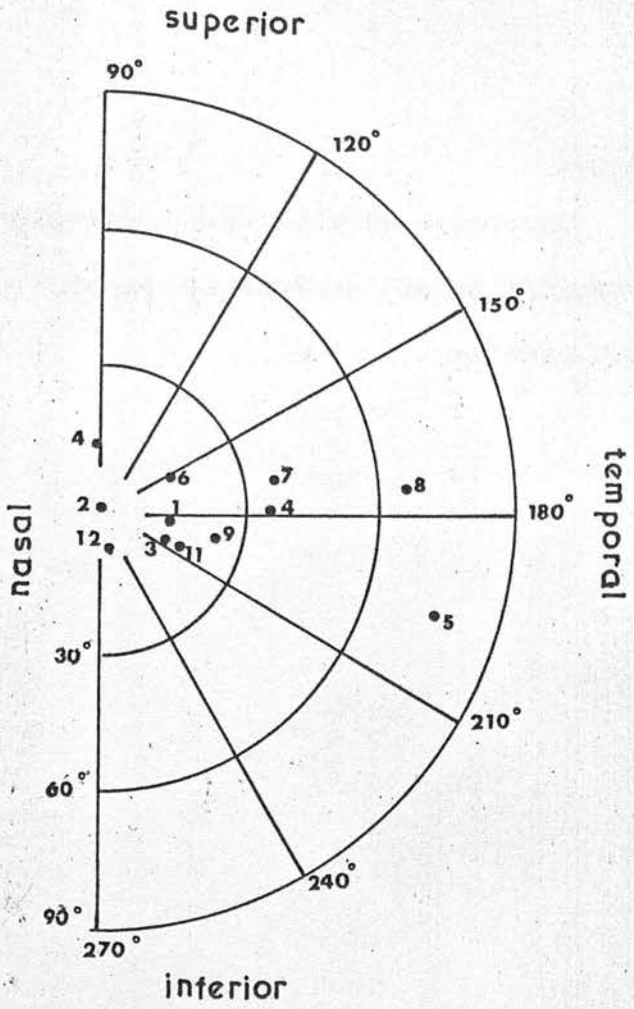
CS20



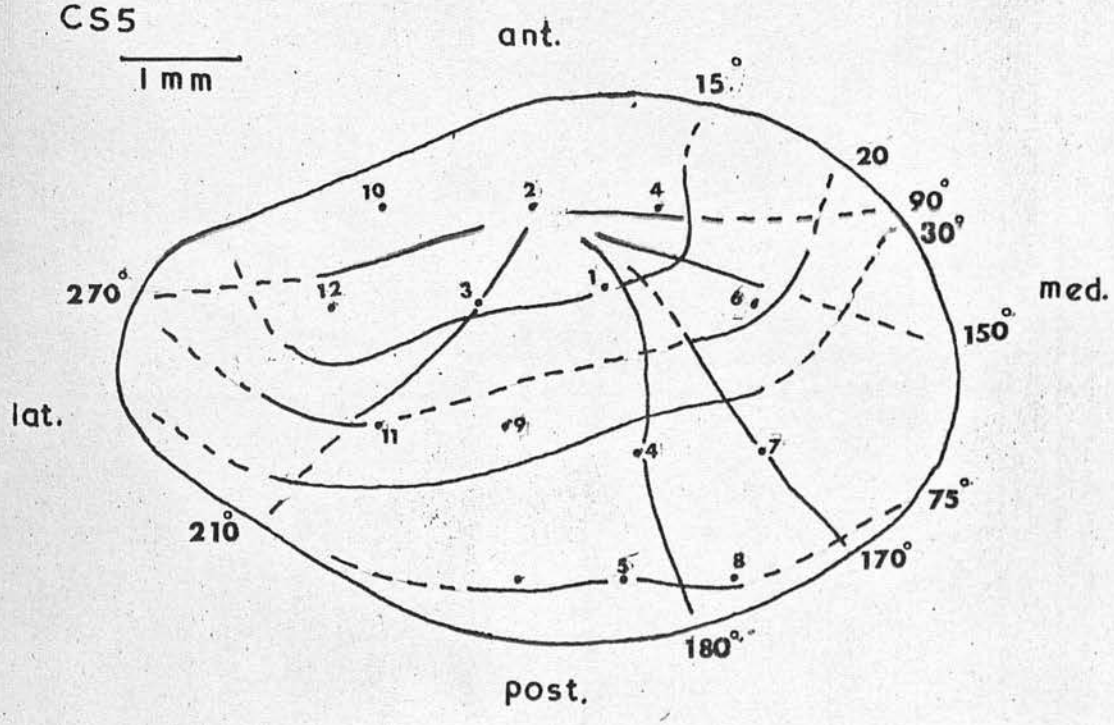
Plane projection of surface of superior colliculus, left.

Fig. 20

Projection of the visual hemi-field of the right eye on the left dorsal surface of the cat's superior colliculus, plane projection (CS5).



Cat, visual hemi-field, right eye



Plane projection of surface of superior colliculus, left.

Fig. 21

Composite results of 5 experiments, to show variation of magnification factors with retinal eccentricity along the horizontal meridian.

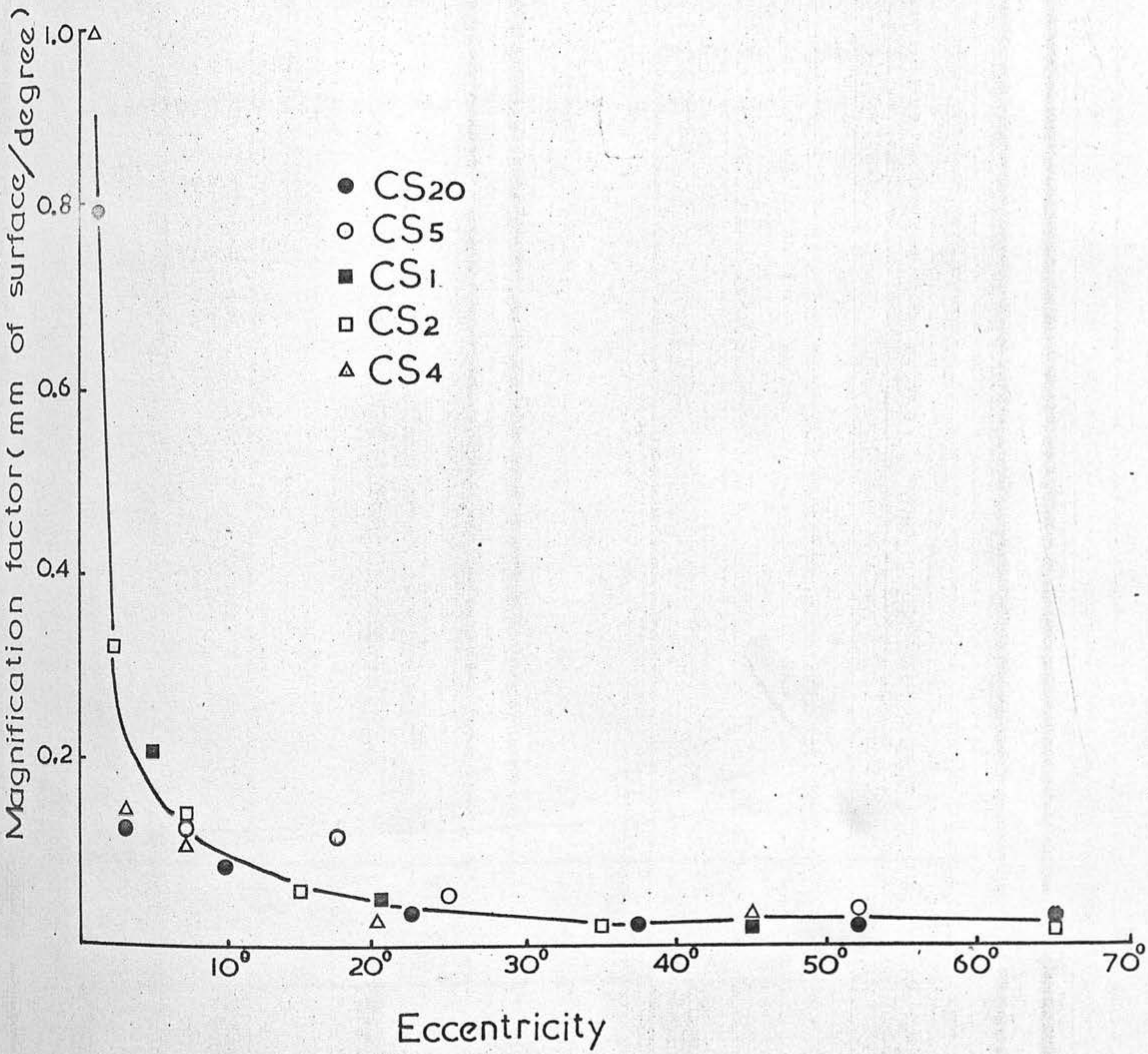

Magnification factor (mm of surface/degree)
1.0
0.8
0.6
0.4
0.2
● CS20
○ CS5
■ CS1
□ CS2
△ CS4
10°
20°
30°
40°
50°
60°
70°
Eccentricity

Fig. 22

Composite curves to show the relationship of the magnification factors of superior colliculus (A), L.G.N. (C), and centro-peripheral ganglion cell density (B) along the horizontal meridian.

(B - reproduced from Stone, 1965; and C - from Seneviratne, 1963).

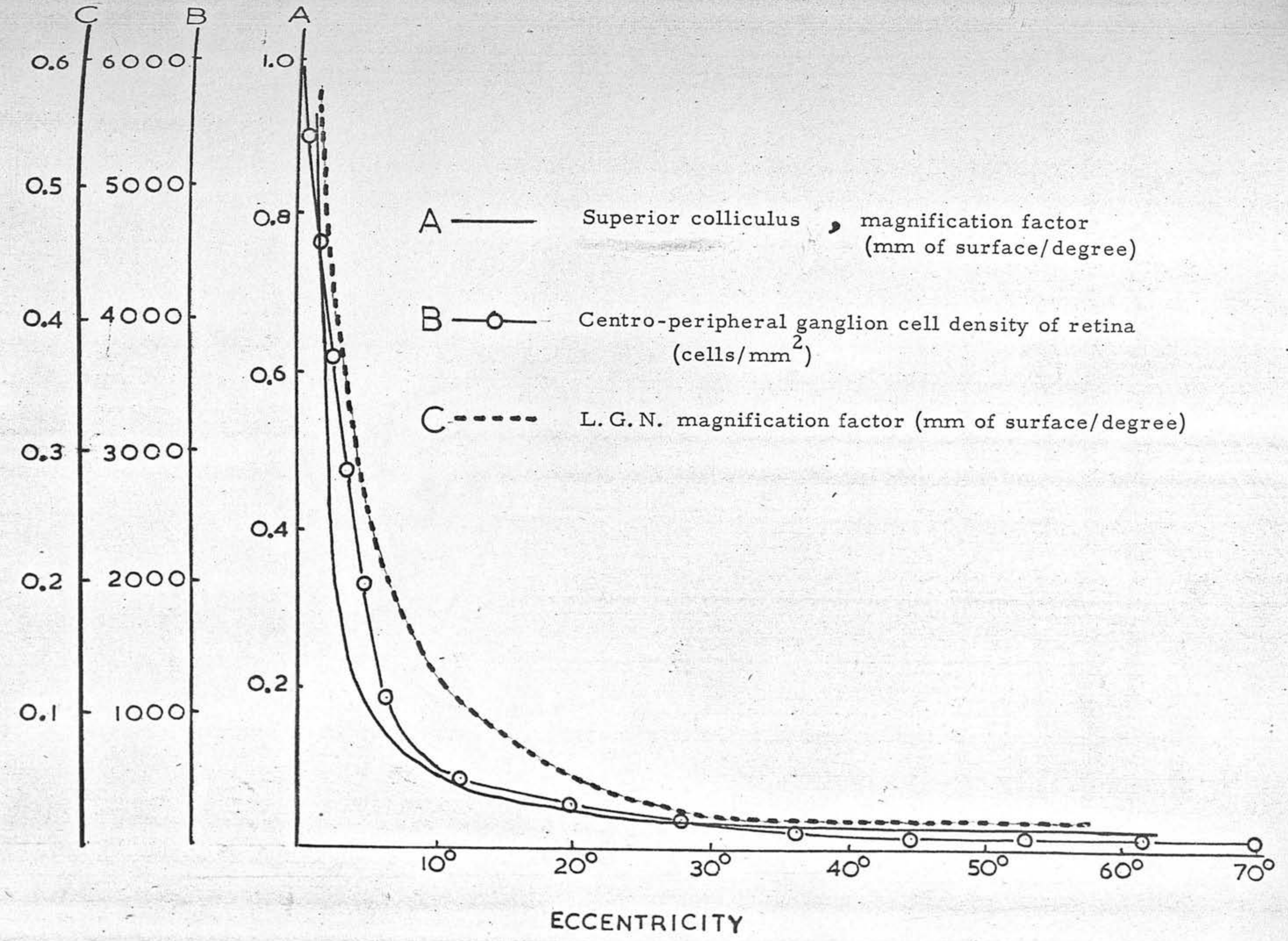
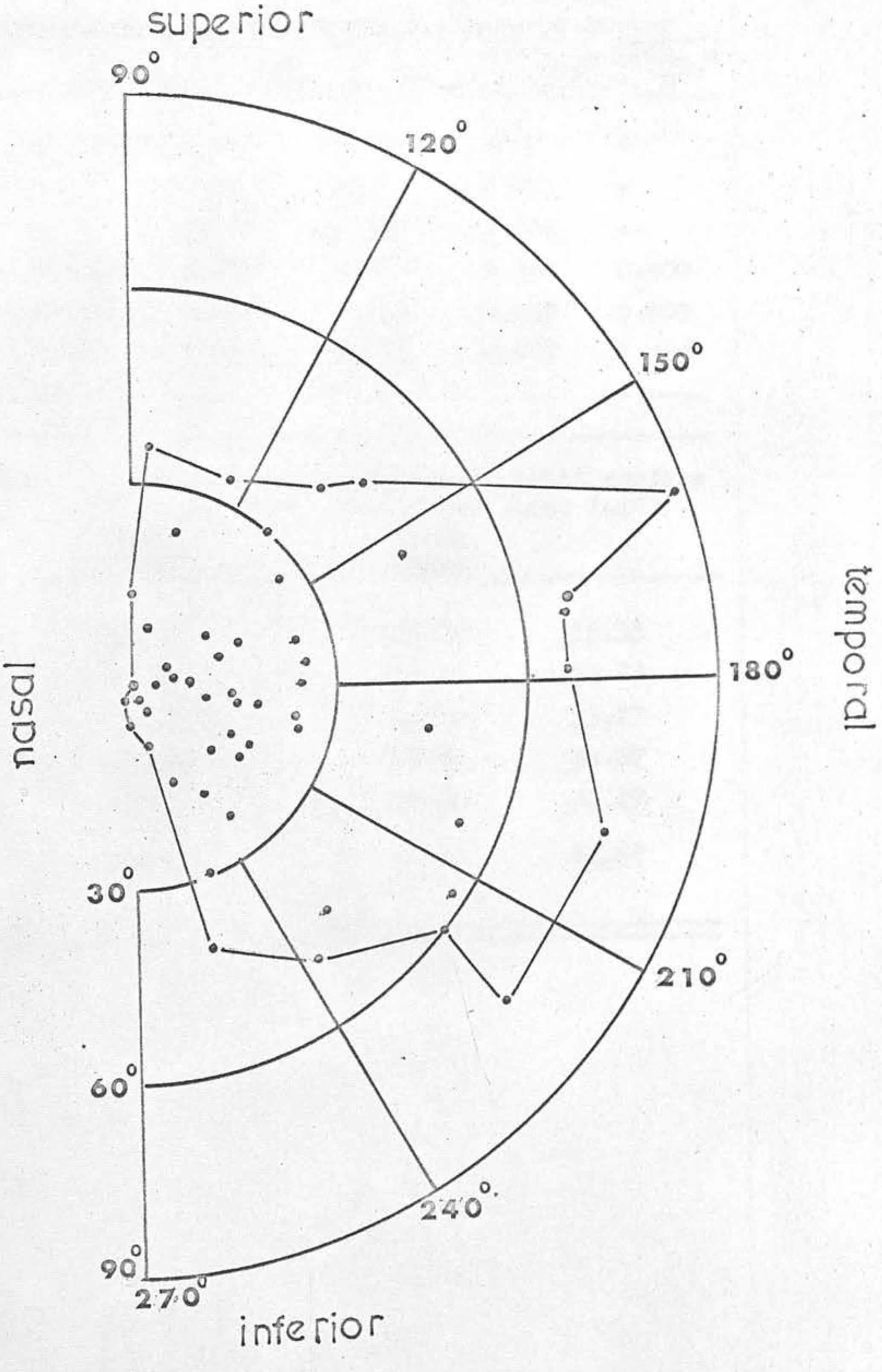

C
B
A
0.6
0.5
0.4
0.3
0.2
0.1
6000
5000
4000
3000
2000
1000
1.0
0.8
0.6
0.4
0.2
A Superior colliculus, magnification factor (mm of surface/degree)
B Centro-peripheral ganglion cell density of retina (cells/mm^2)
C L. G. N. magnification factor (mm of surface/degree)
10°
20°
30°
40°
50°
60°
70°
ECCENTRICITY

Fig. 23

Composite results of 5 mapping experiments, to show the distributions of receptive field centers. The line joins the most peripheral points obtained.



Cat, visual hemi-field, right eye.

Table 2: showing the surface area of the superior colliculus representing different sectors in the visual field.

Expt.	surface area as % of total / degree of sector					
	90°-120°	120°-150°	150°-180°	180°-210°	210°-240°	240°-270°
CS1	0.405	-	-	0.767	-	-
CS2	-	-	0.407	0.247	0.733	-
CS4	-	-	0.560	0.609	0.400	-
CS5	0.130	0.130	0.847	1.100	0.300	0.300
CS20	0.300	0.213	0.547	0.567	0.260	0.400
Average	0.278	0.172	0.590	0.658	0.423	0.350

Expt.	body wt. (kg.)	surface area (% of total)		total surface area (mm^2)
		upper field	lower field	
CS1	2.8	39.17	60.83	33.53
CS2	2.9	45.64	54.36	33.67
CS4	2.2	41.20	58.80	33.27
CS5	2.6	42.70	57.30	34.67
CS20	2.5	41.40	58.60	33.27
Average	2.6	42.02	57.98	33.68

Table 3: showing the surface areas of the S.C. (as % of the total) subserving different semi-circles in the visual field.

Eccentricity	CS1	CS2	CS4	CS5	CS20	Average
$0^{\circ}-2^{\circ}$	-	-	9.4	-	12.6	11.00
$0^{\circ}-5^{\circ}$	-	12.2	22.6	-	21.0	18.60
$0^{\circ}-10^{\circ}$	20.6	24.4	33.6	-	-	26.20
$0^{\circ}-15^{\circ}$	-	-	-	24.0	37.0	30.33
$0^{\circ}-30^{\circ}$	45.8	41.6	56.2	59.9	52.8	51.26
$0^{\circ}-60^{\circ}$	77.8	-	84.8	-	84.6	82.40

Table 4. Classification of units recorded in the superior colliculus.

No.	Type of unit	Receptive field size (degree)	Main characteristics	Numbers of unit	%
1	Small receptive-field unit	2° (0.5°-3.0°)	slow movement(.5°-2.0°/sec in any direction	51	34.00
2	Medium receptive field unit	3° to 10°	moderate movement (5.0°-40° / /sec) in any direction	34	22.67
3	Large receptive field unit	over 10° to 40°	fast movement(100°-300°/sec) in any direction	32	21.33
4	Directionally selective unit		movement in particular direction	21	14.00
5	Specific orientation unit		movement in particular orientation	12	8.00

Fig. 24

Histogram showing distribution of units recorded from different layers of superior colliculus; Stratum griseum superficiale - upper half (a), and lower half (b), Stratum opticum - upper half (c) and lower half (d), and Stratum griseum intermediale - upper half (e) and lower half (f); small receptive field unit (I), medium-sized field unit (II), large receptive field unit (III), directionally selective unit (IV), and specific orientation unit (V).

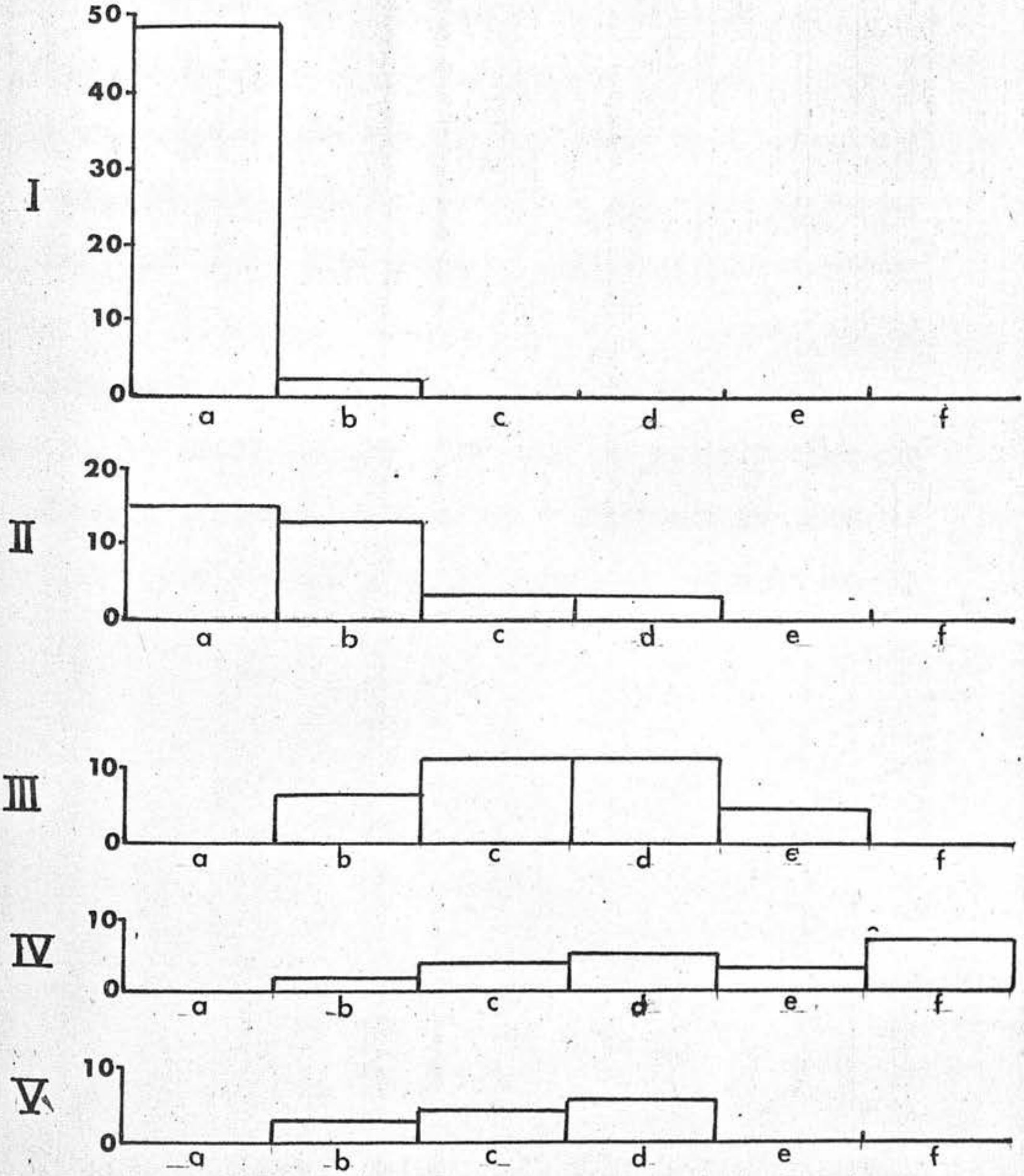

I
50
40
30
20
10
0
a
b
c
d
e
f
II
20
10
0
a
b
c
d
e
f
III
10
0
a
b
c
d
e
f
IV
10
0
a
b
c
d
e
f
V
10
0
a
b
c
d
e
f

Fig. 25

Diagram to illustrate the behaviour of units recorded in the superior colliculus.

The sizes of the receptive fields and their behaviour in responding to moving stimuli are shown on the left. The broken line represents an approximate boundary of the receptive field and the arrow indicates the direction of movement of a stimulus. A scale of a receptive field is 10° in size.

The distribution of units in the superior colliculus corresponding to the type of receptive field on the left is shown on the right side as a diagrammatic cross section of the superior colliculus with a scale 1 mm.

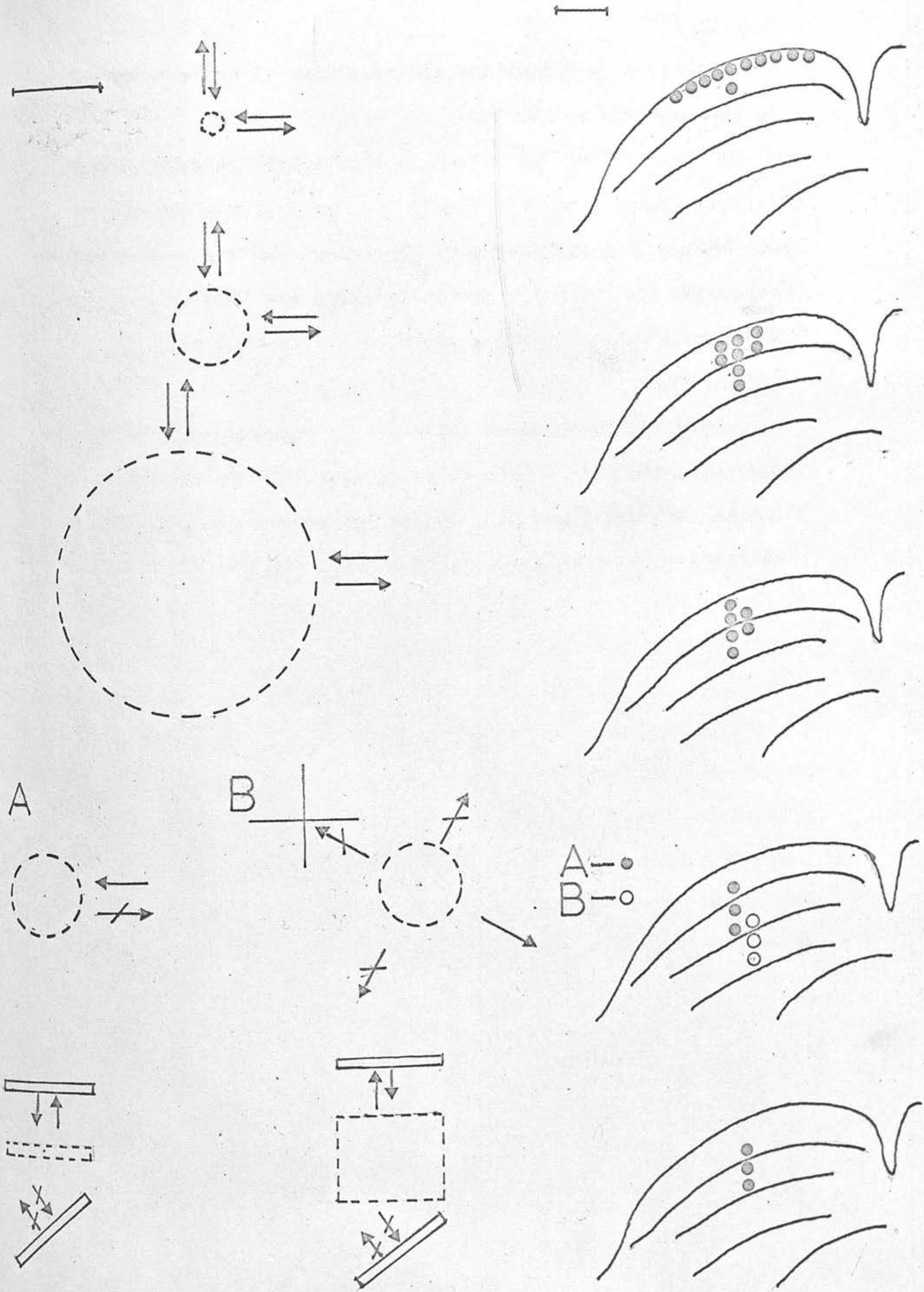

A
B
A
B

Fig. 26

(a) Shows the latencies of the single unit responses by a neon flash placed at the perimeter arm, being 33 cm. from the eye. This unit was on 12°-195°, and responded only to movement in a centrifugal direction. The latencies are 31.6, 34.7, and 42.1 msec from left to right. Note the progressive increase in latency in the second and third response. Time 10 msec in each record. (CS27).

(b) Shows the responses of a directionally selective unit to a rectangular light-bar 10° x 3° moving up and down across the receptive field. The velocity was approximately 30°/sec. This unit had a receptive field about 10° in size, positioned on 35°-206°, and was recorded from the lower part of the stratum opticum. The arrow indicates the direction of movement. (CS13). Time, 100 msec.

(c) A light-bar 1/2° wide crosses the receptive field 2° in diameter with a slow speed about 1°/sec. Increasing the width of the stimulus greatly reduces the response. No preferential direction was observed in this unit. The unit had a receptive field 2° in diameter, and was obtained from the upper part of the stratum griseum superficiale, and positioned on 15°-228°. (CS10). Time, 100 msec.

Fig. 26 (cont.)

(d) shows the unit response of a medium-sized receptive field to 'on' and 'off' excitation with a 10 mm light spot. The middle trace is a signal from a photocell placed in the center of the receptive field, 'on' is away from the spike potentials. The unit had a receptive field 5° in diameter, being recorded from 12°-204° in the visual field. Time, 10,000 msec. (CS14)

(e) Response of another medium-sized receptive field unit to a moving rectangular light-bar of 10° x 2° in size and approximately 30°-50°/sec. This unit was recorded from the lower part of the stratum griseum superficiale, and was on 18°-225°. Time, 100 msec. (CS22).

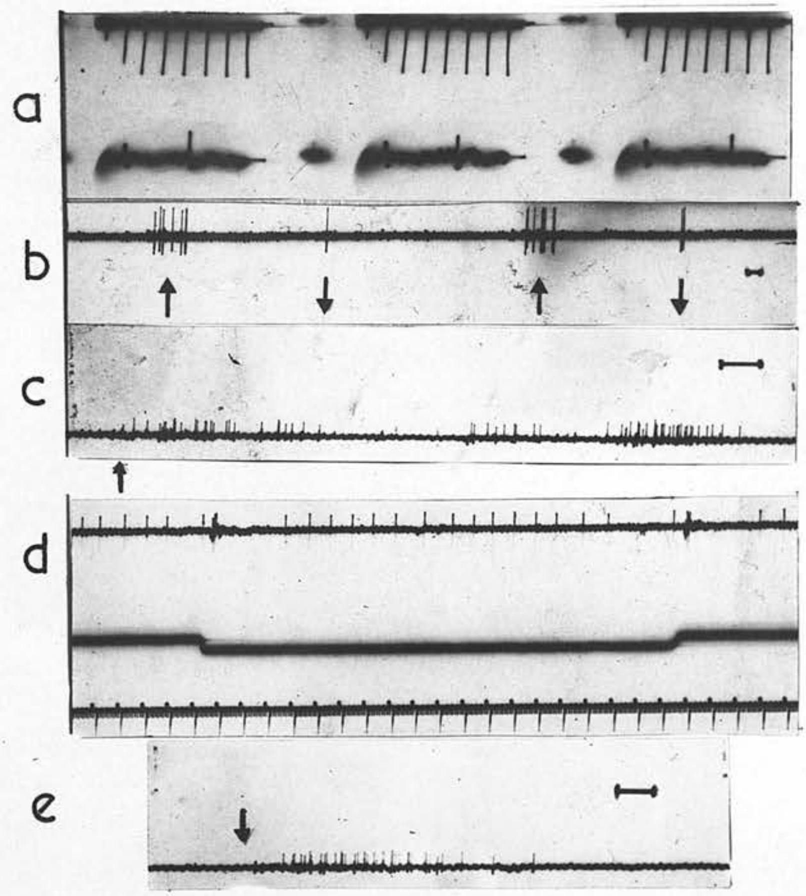

a
b
c
d
e

Fig. 27 shows the responses of large receptive field units.

(a) 'on' and 'off' responses to 10 mm spot of light. For the photocell's signal, 'on' is away from the spike potentials. This unit had a receptive field about 15° in diameter, being recorded from the lower part of the stratum opticum. The center of the field was on 15°-216°. Time, 10,100 msec. (CS21).

(b) Responses of the large receptive field unit to fast movement. The rate of movement was 240°/sec, measured by two photocells placed in the receptive field 20° apart. This unit, positioned on 23°-189°, was recorded from the upper part of the stratum opticum and responded to fast movement in every direction. Time, 100 msec. (CS11).

(c) Another large receptive field unit, being recorded from the stratum griseum superficiale, responded to a rectangular light bar 10° wide and 5° thick moving across the receptive field at the optimum rate of 150°/sec. The range of velocity varied from 60°-350°/sec. A slower or faster rate than this gave no response. The region from which the responses could be elicited covered a large area, about 40° across, but the center was approximately on 10°-180°. No preferential direction was observed in this unit. The arrow indicates, approximately, the stimulating point. Time, 10 msec. (CS24).

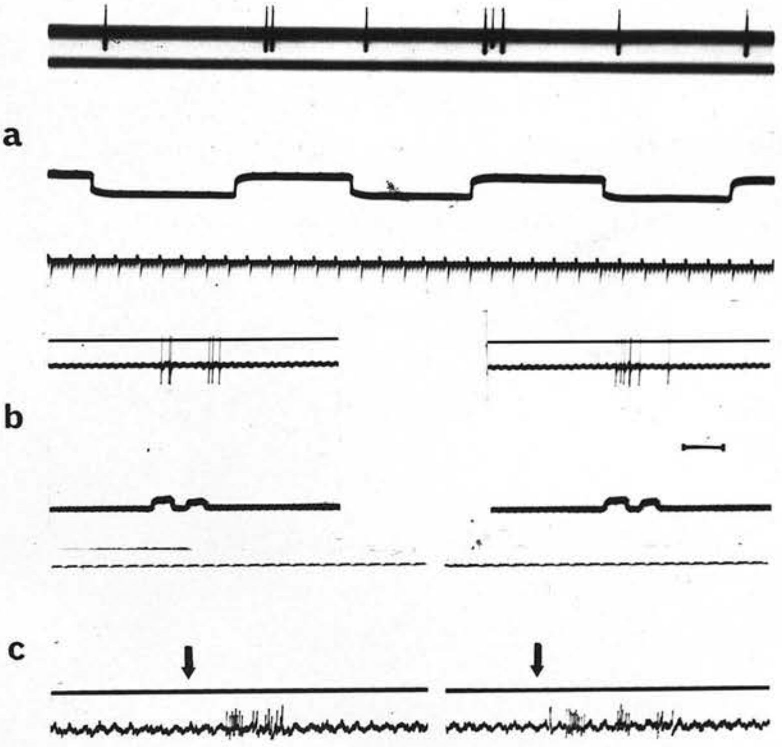
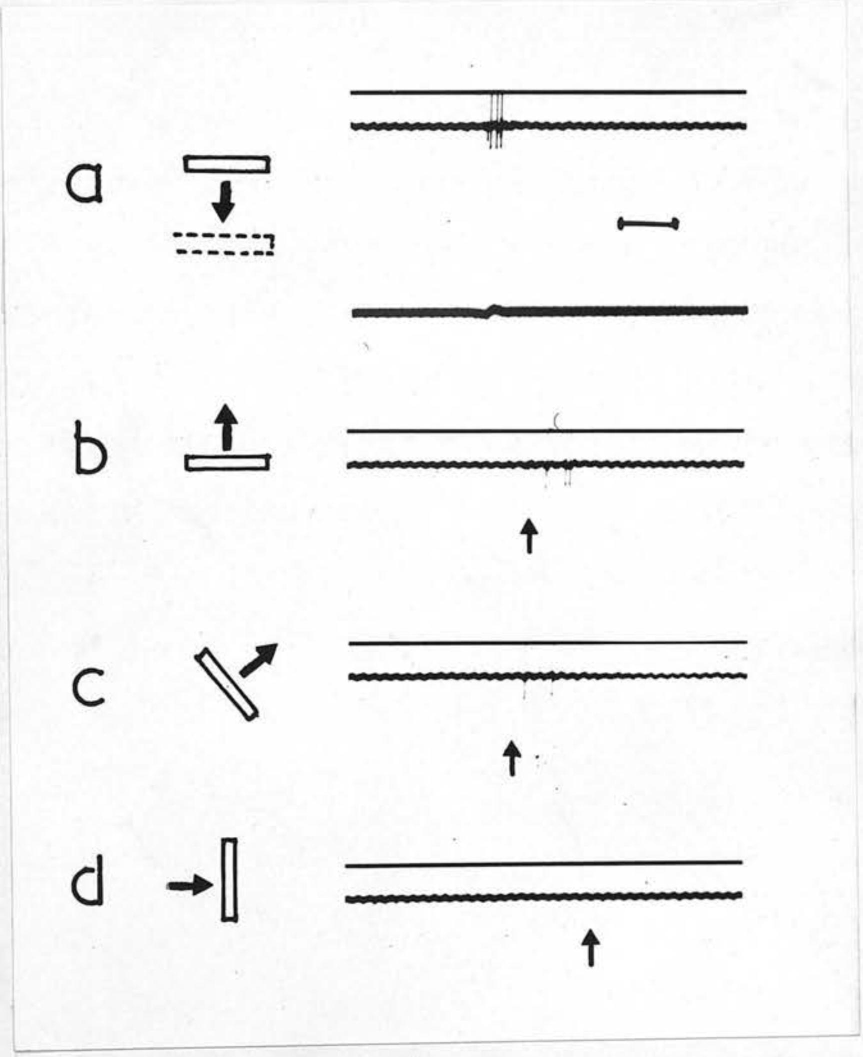

a
b
c

Fig. 28

(a) Responses of specific orientation unit to moderate movement of rectangular, 5° X 1°, light-bar in different directions. The upper two records show the responses from optimally orientated position of stimuli moving back and forth across the receptive field. Tiling the stimulus renders it ineffective in the lower two records. This unit is situated on 4°-210°. The small arrow indicates the approximate point of stimulation, while the large one indicates the direction of motion. Time, 100 msec. (CS11).

(b) Shows responses of another specific orientation unit to movement in different directions. This unit had a receptive field 8° X 10° in size, being recorded from the upper part of the stratum opticum, positioned on 26°- 188° The optimum stimulus was found to be a slit of light about 10° wide and 1° thick. This unit responded well if the slit was moved steadily across the receptive field and sustained discharges were evoked over the entire length of the field. The rate of movement was about 20°/sec. Time, 100 msec. (CS11).

A



B

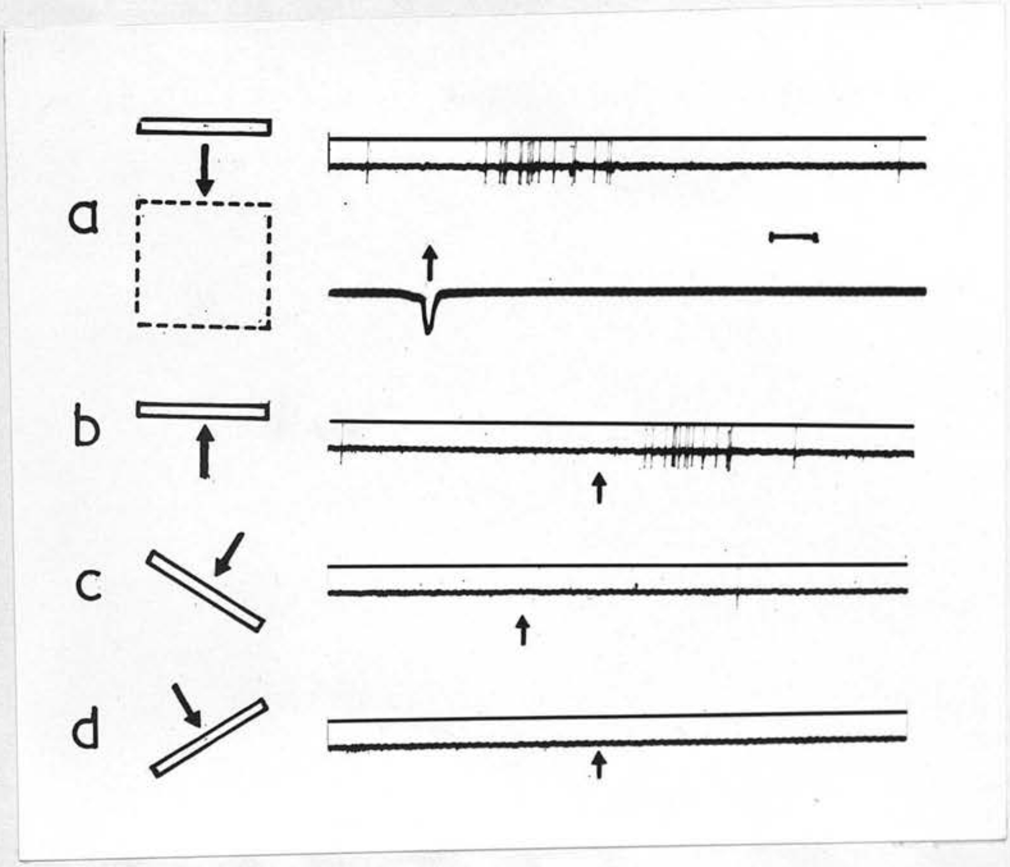


Fig. 29

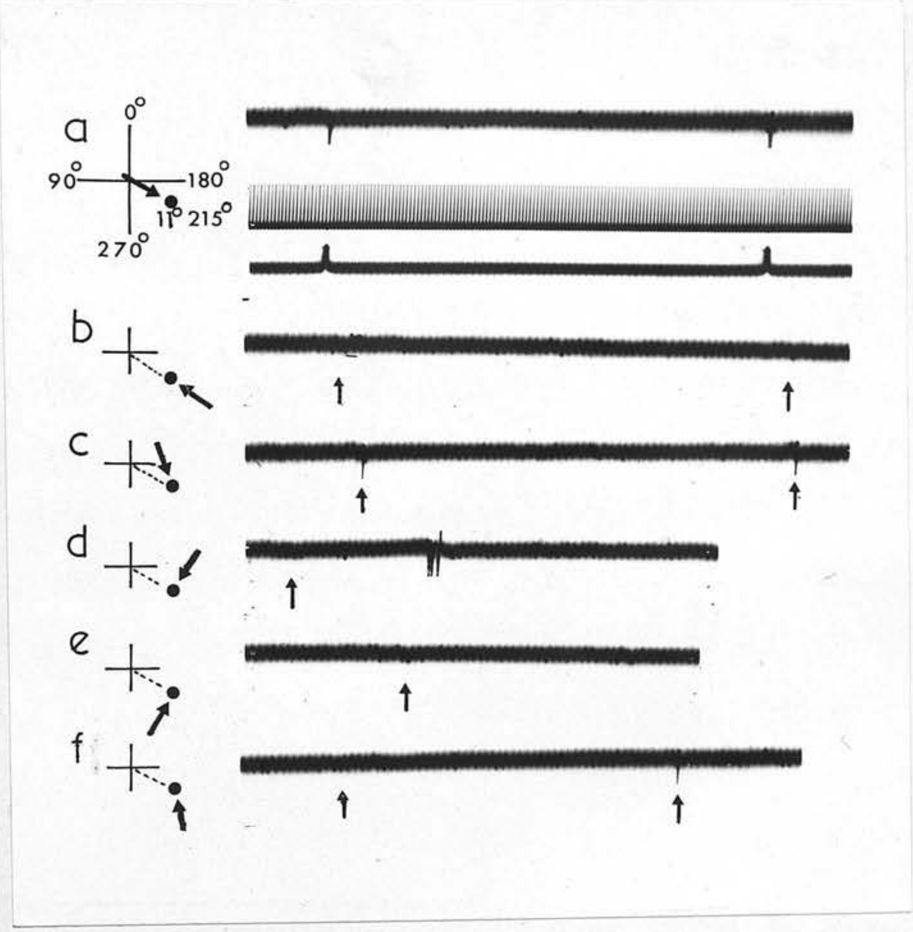
Shows responses of a directionally selective unit to movements of different directions. This unit had a receptive field size about 10° in diameter; was recorded from the lower part of the stratum griseum intermediale, and had a receptive field center at 11°-215°. The optimum rate of movement was 100°-150°/sec. Time, 10 msec. (CS27).

Note the best response in the top record which was obtained from movement in a centrifugal direction. The responses could be elicited in a certain range of directions; and note also the artifact in record (d).

Fig. 30.

Another directionally selective unit which gave a response only to movement in a centrifugal direction within a certain range of directions. Tilting the stimulus 45° above the best direction diminished the responses and gave even less or none in the direction perpendicular to the centrifugal direction. Velocity used in this case was 200°-300°/sec. Time, 10 msec. This unit was again recorded from the stratum griseum intermediale, and was on 20°-230°. (CS26).

29



30

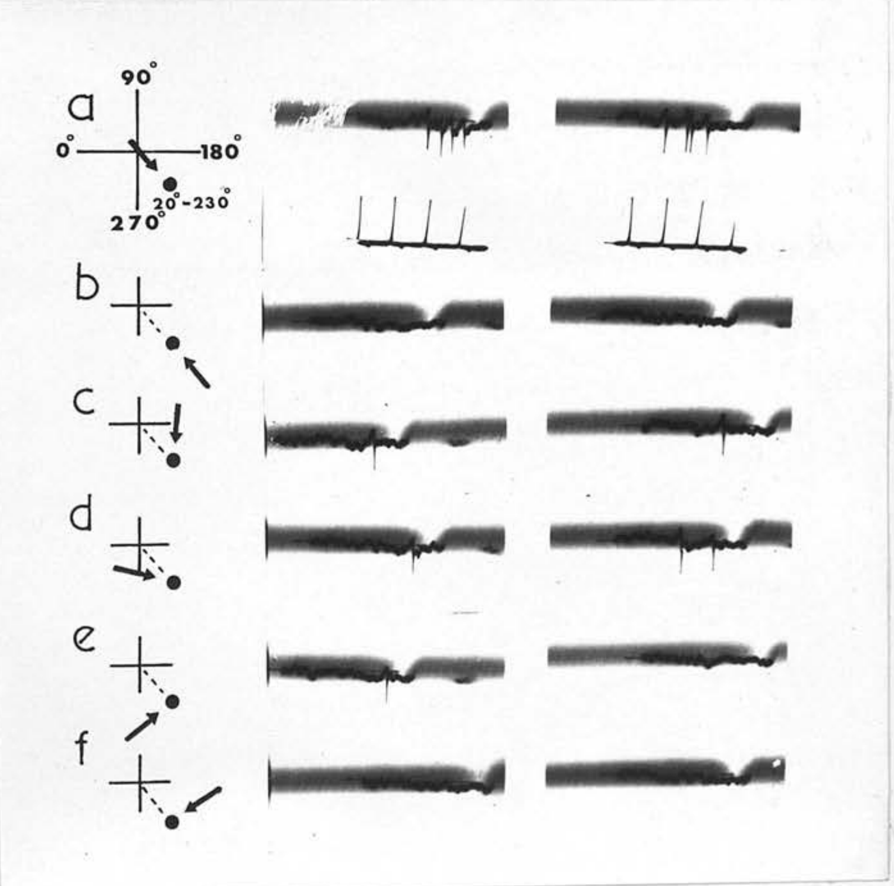


Fig. 31

The upper series of records (a., b., and c.) show the effect of cooling the corresponding part of the visual cortex upon the visual responses in a single unit of the superior colliculus.

(a) Response of a unit in the upper part of the stratum opticum, positioned on 15°-206°, having a receptive field size of 3° X 10°, to movement of a slit of light 1° X 10° across the receptive field with a speed of 25°/sec. This unit responded to movement back and forth across the receptive field; tilting of the direction of the stimulus on either side more than 30° gave no response.

The middle trace in (a) shows the signal from two photocells, 10° apart, for measuring the velocity of the stimulus. Time 10,100 msec in the lower trace. (CS 8)

(b) After cooling the corresponding part in the visual cortex to about 10°C for 2.5 min, the visual response disappeared and only the spontaneous activity still remained.

(c) The visual response recommenced when the cooling was discontinued.

Time in each record (b) and (c), same as in (a).

The lower series shows the responses of another unit to cooled visual cortex, the same procedure as in the upper series.

(d) This unit responded to fast movement with black card-board 10° wide and 2° thick moving across the receptive field in every direction. The region from which the responses were evoked was about 20° across with approximate center at 40°-197°. Again, this unit was recorded from the upper part of the stratum opticum.

(e) A record, with cooled cortex, showing complete absence of visual response after 5 min. cooling. The visual response came back after cooling had been stopped.
Time 10 msec in each record. (CS 8)

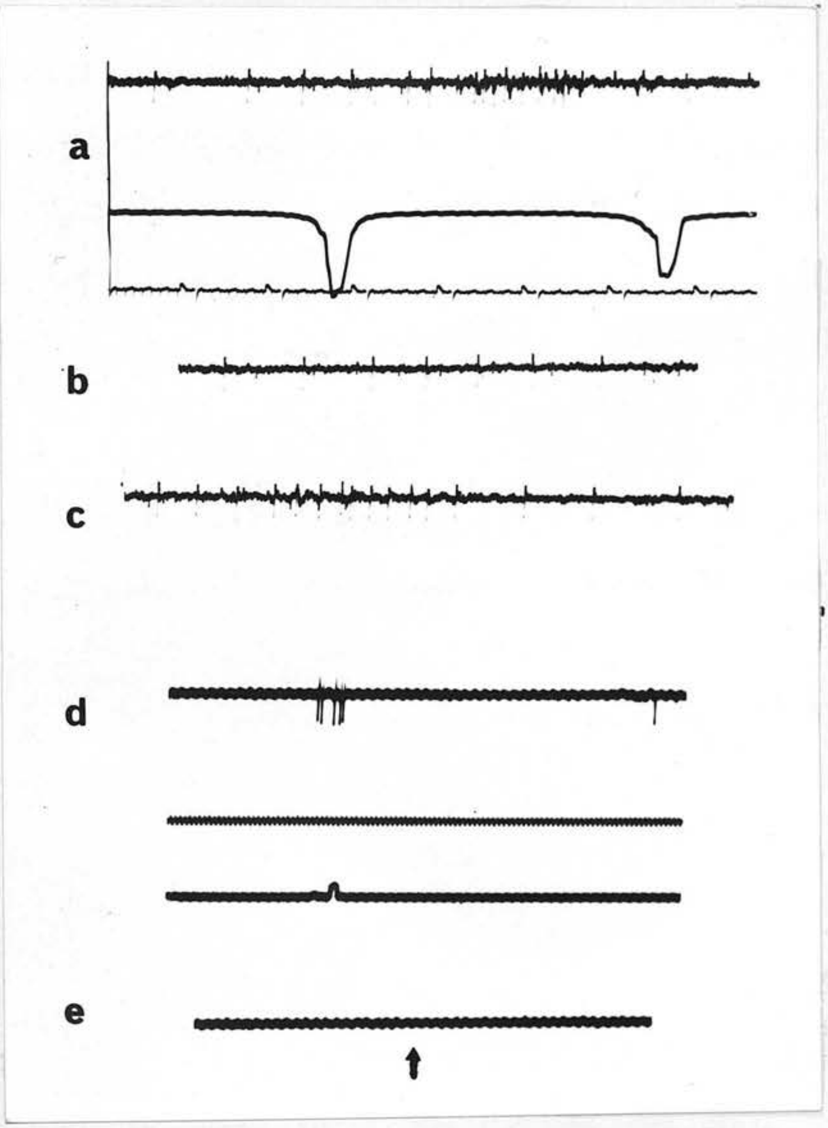
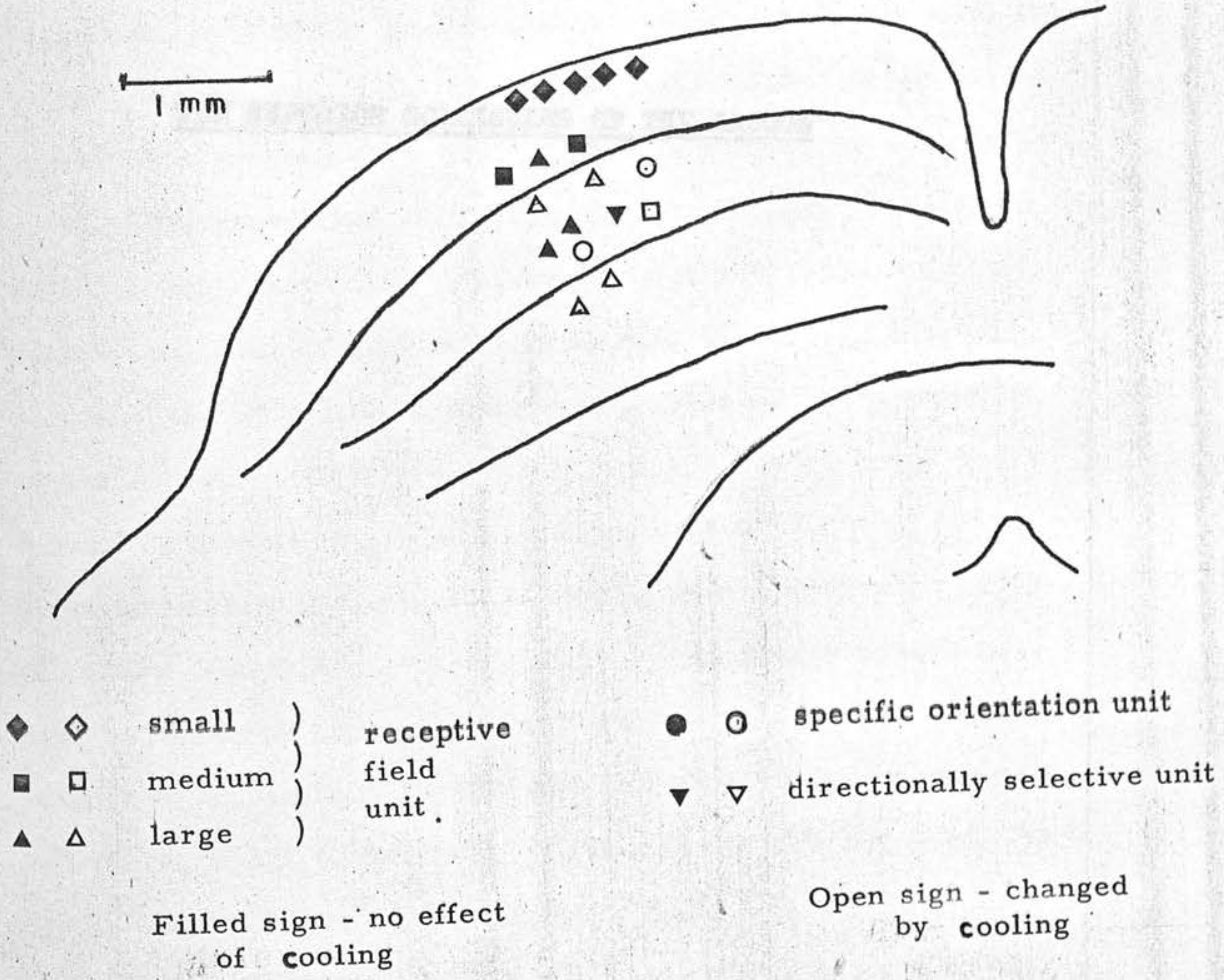

a
b
c
d
e

Fig. 32

Diagramatic transverse section of superior colliculus illustrating the effect of cooling the corresponding part of the visual cortex upon single unit activity on the superior colliculus, with results of 6 experiments superimposed.


1 mm
◆ ◇ small
■ □ medium
▲ △ large
receptive field unit.
Filled sign - no effect of cooling
● ○ specific orientation unit
▼ ▽ directionally selective unit
Open sign - changed by cooling

THE SUPERIOR COLLICULUS OF THE BABOON

III. THE SUPERIOR COLLICULUS OF THE BABOON

A. THE RETINAL REPRESENTATION ON THE SURFACE OF THE SUPERIOR COLLICULUS

Out of 5 baboons, 3 successful mapping experiments have been done. The plane projections of the visual field onto the surface of the S.C. which has been flattened out in order to correct the curvature of the surface, have been illustrated in Fig. 34, experiment MS5; Fig. 35, experiment MS2; and Fig. 36, experiment MS4. Figure 34 is a projection of the left visual hemi-field onto the surface of the right S.C., whereas Fig. 35 and 36 are the projections of right visual hemi-field onto the surface of left S.C.. The size of the baboon's superior colliculus, unlike that of the cat's, shows considerable variations. Owing to the different sizes of baboon used in this study, there is no simple relation between the size of the S.C. and the animal's weight. Baboons used in experiments MS2, MS4, and MS5 whose body weights are 4.5, 5.77, and 8.00 kg. have collicular surface areas of 28.00, 43.06, and 47.93 mm^2 respectively (Table 5).

The general scheme of retinotopic projection onto the surface of the S.C. (Fig. 34, 35 and 36) has confirmed the pattern of the retinotopic organization of mammals in general.

This consists of representation of the central area of the retina in the anterior pole with the peripheral field posteriorly; the horizontal meridian (0°-180°) runs backward and slightly medially, the vertical meridians anteriorly, the upper vertical meridian (0°-90°) medially, and the lower vertical meridian (0°-270°) laterally.

Among the three maps, the detail of retinotopic projection has been shown only in the experiment MS5. In spite of this, all 3 maps show clearly that the ratio of the surface areas of the lower and upper field quadrants as divided by a horizontal meridian (0°-180°) is about 1:1 (Table 5) in contrast to 1.5:1 obtained in the cat's superior colliculus.

B. THE MAGNIFICATION FACTOR

The results also establish that the central field occupies an area larger than the peripheral field. The area within 20° occupies about half of the total surface area.

The magnification factor, as mm. of surface of receptive area per degree of the visual field (Daniel and Whitteridge, 1960) has been calculated along the horizontal meridian (0°-180°) and has been plotted against the retinal eccentricity (angular deviation from the fixation point, Fig. 38). The magnification factor falls rapidly within 5° from the center of fixation and declines gradually toward the periphery.

The maximal value of the magnification factor at the center is about 0.75 mm./degree; and the value 0.07, and 0.03 at 15° and 40° from the fixation point respectively.

The relationship of the magnification factors of the S.C., visual cortex (Daniel and Whitteridge, 1960) and centroperipheral ganglion cell density (Whitteridge, unpublished observations) as plotted against the retinal eccentricity has also been shown in Fig. 39. In general, there is a close correlation of these 3 curves with some minor differences which are regarded as unimportant when the technical error and number of sample are taken into account.

Owing to the technical difficulty in approaching the surface of the S.C., only 3 mapping experiments have been done. The extent of the visual field as plotted by using the point of localization in the visual field is shown in Fig. 37. The peripheral field along the horizontal meridian has been recorded up to 60°-70° from the center of fixation, but the upper and lower visual fields near the vertical meridians show restricted representation. By examining the surface areas of the reconstructed S.C., it appears that some of the surface areas have not been explored in the course of the experiments.

In addition to the peripheral extent of the visual field just described, the experiment also shows that there is a representation of a fovea onto the S.C., at least in one experiment (Fig. 34, MS5), in which a point of localization was exactly on the center of fixation, and the area within 2.5° in this experiment occupies about 18% of the total surface area.

C. SINGLE UNIT OBSERVATIONS

In the course of mapping experiments, 8 single units have been observed and some of the characteristics and sites of recordings are summarized in Table 6. Although the sample is very small, most of the units, like those in the cat's superior colliculus, responded well to moving stimuli. Anatomically, the units were obtained from 3 layers, 5 units from the stratum griseum superficiale, 1 from the stratum opticum and 2 from the stratum griseum intermediale. Apart from the non-directionally selective small receptive field units about 3°-5° in diameter, two specific orientation units recorded from the stratum griseum superficiale and stratum opticum were found. (Fig. 40).

The latencies of multiunit responses by neon flash placed at the perimeter arm have been measured and the mean value of about 30 msec obtained, compared with the latency of about 40 msec. of the striate cortex, with more or less the same stimulus parameters.

Fig. 33

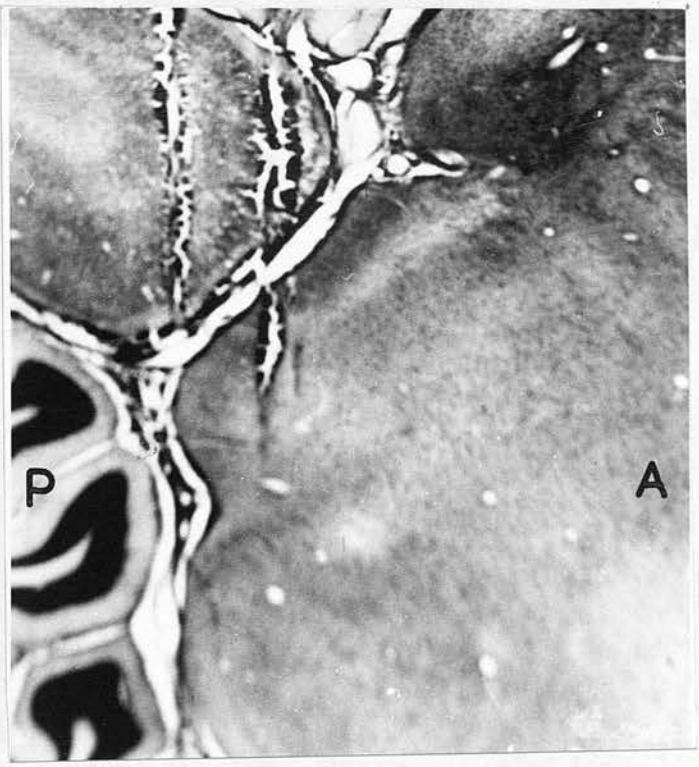
(a) Photomicrograph of a parasagittal section of baboon's superior colliculus to show the electrode tracks. The animal's head is in the Clarke-Horsley plane.

Section magnification X 12.

(b) The same as (a) but higher magnification.

Section magnification X 18

a



b

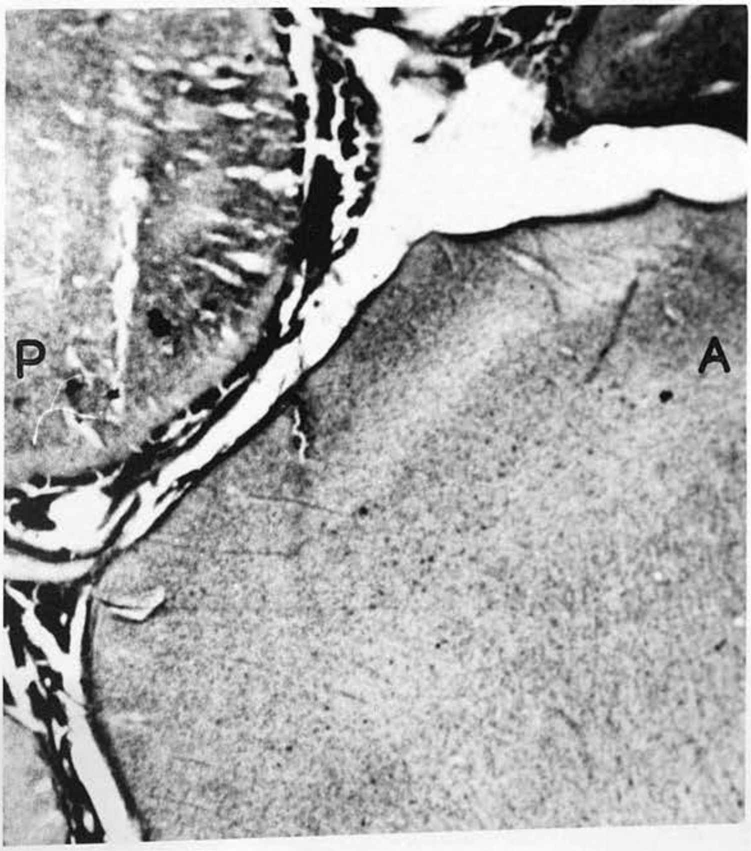
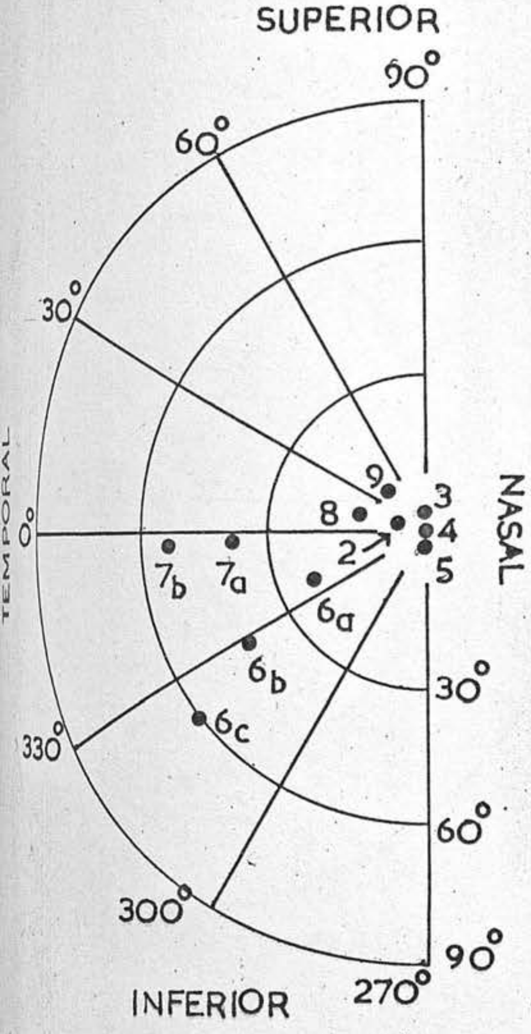
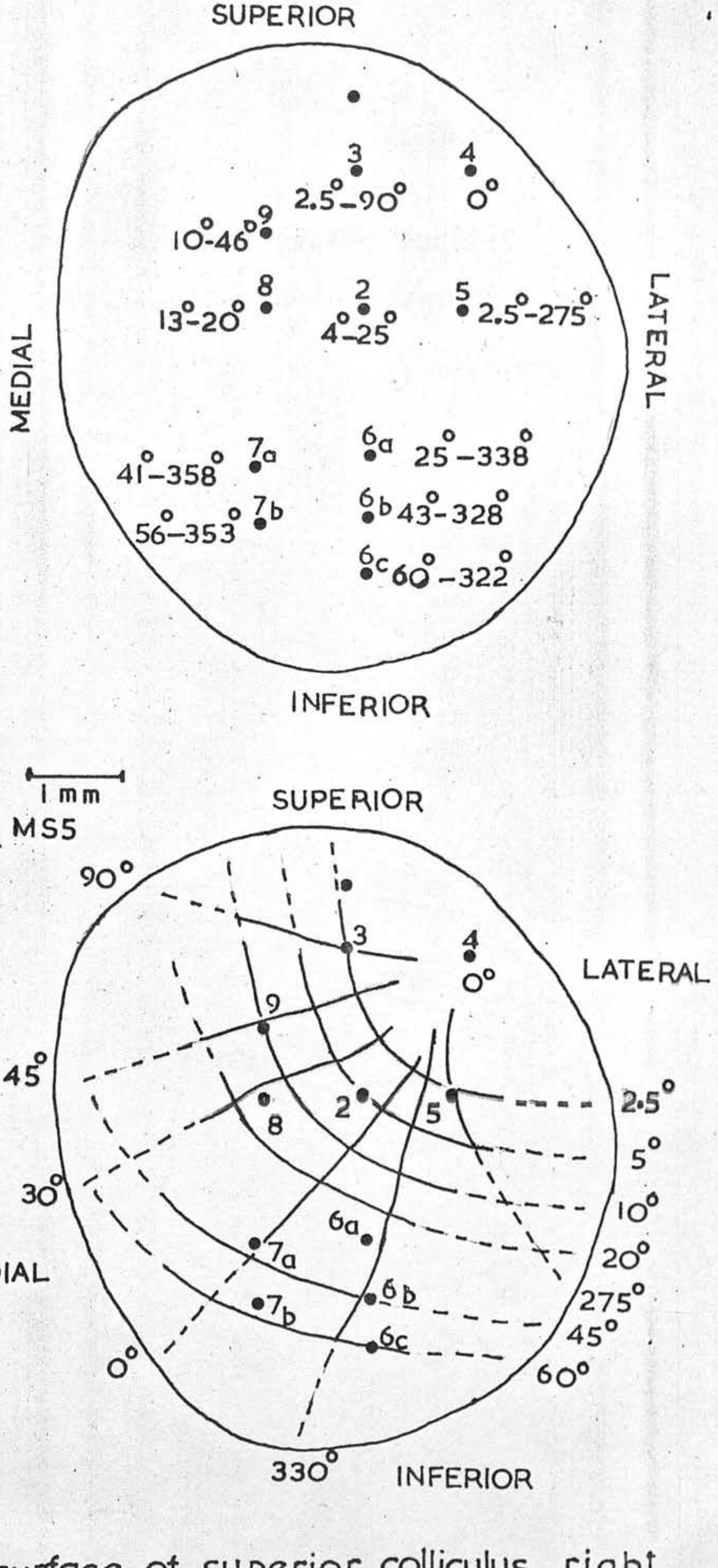


Fig. 34

Projection of the visual hemi-field of the left eye on the surface of the baboon's right superior colliculus, plane projection (MS 5).



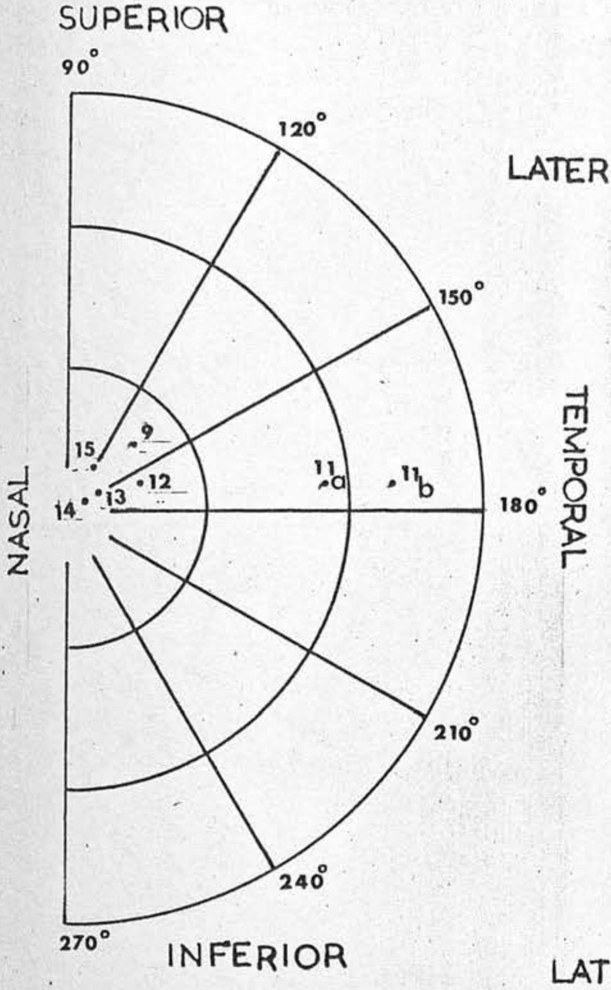
Baboon, visual hemi-field, left eye.



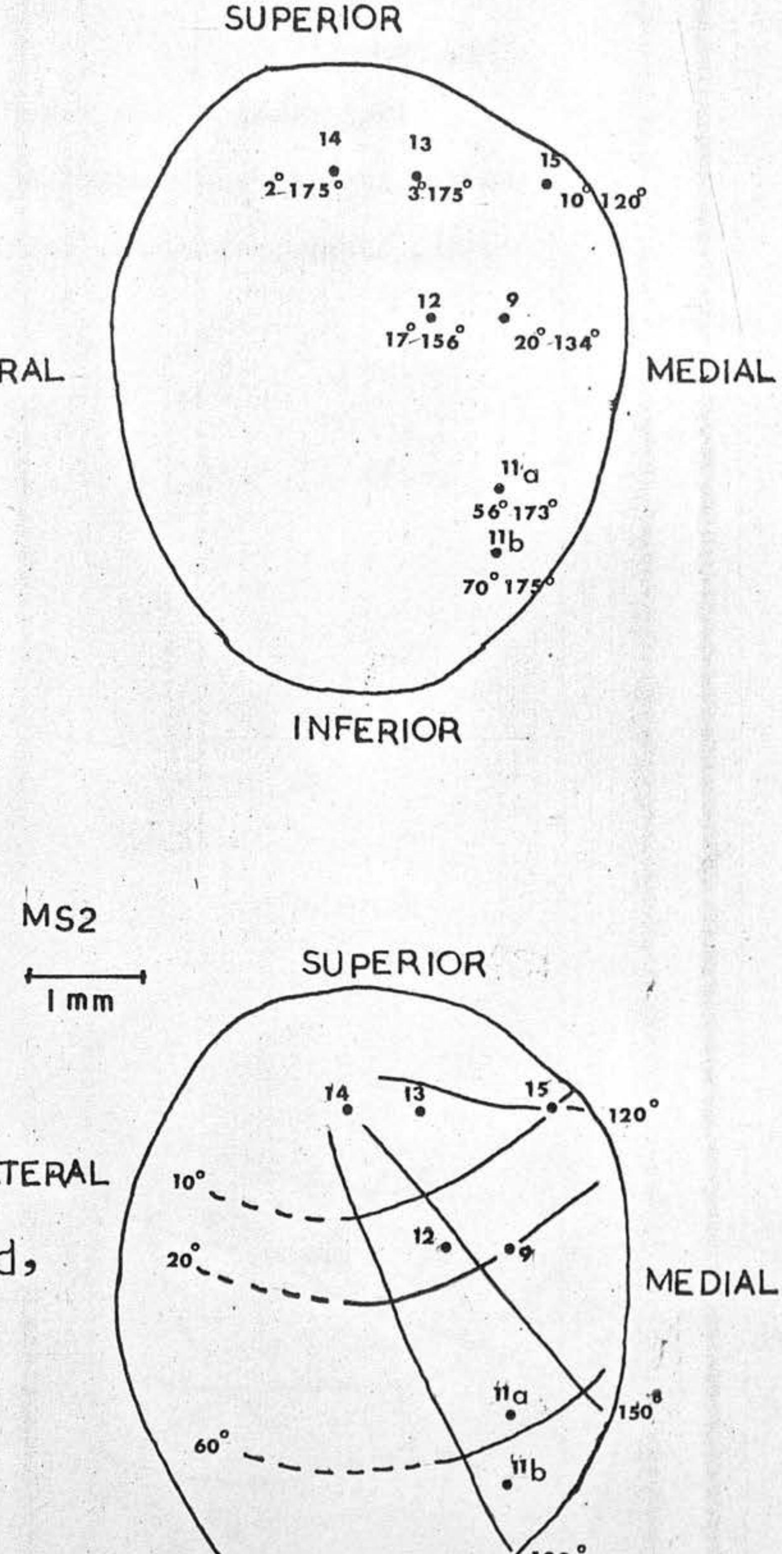
Plane projection of surface of superior colliculus, right.

Fig. 35

Projection of the visual hemi-field of the right eye on the left dorsal surface of the baboon's superior colliculus, plane projection (MS2).



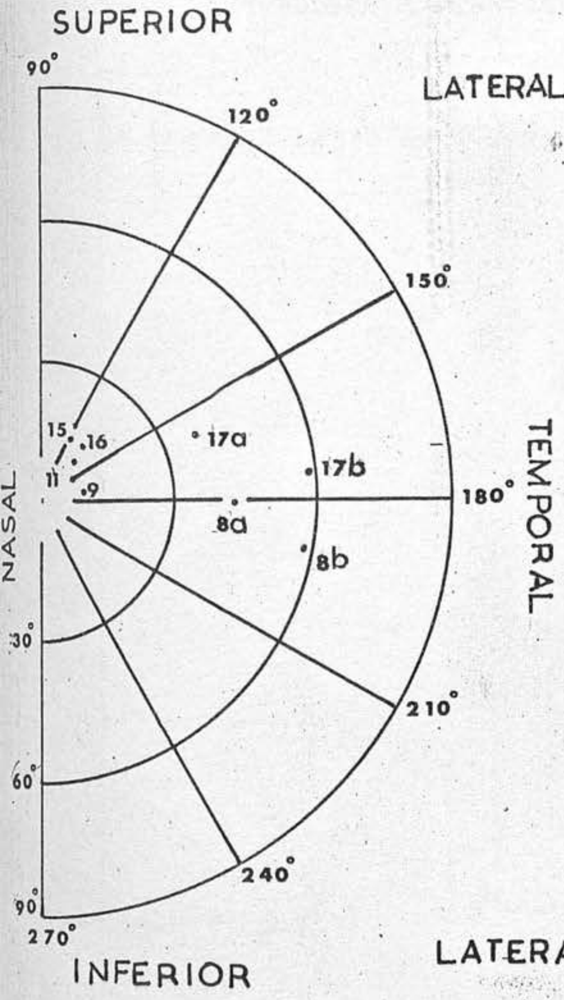
Baboon, visual hemi-field, right eye.



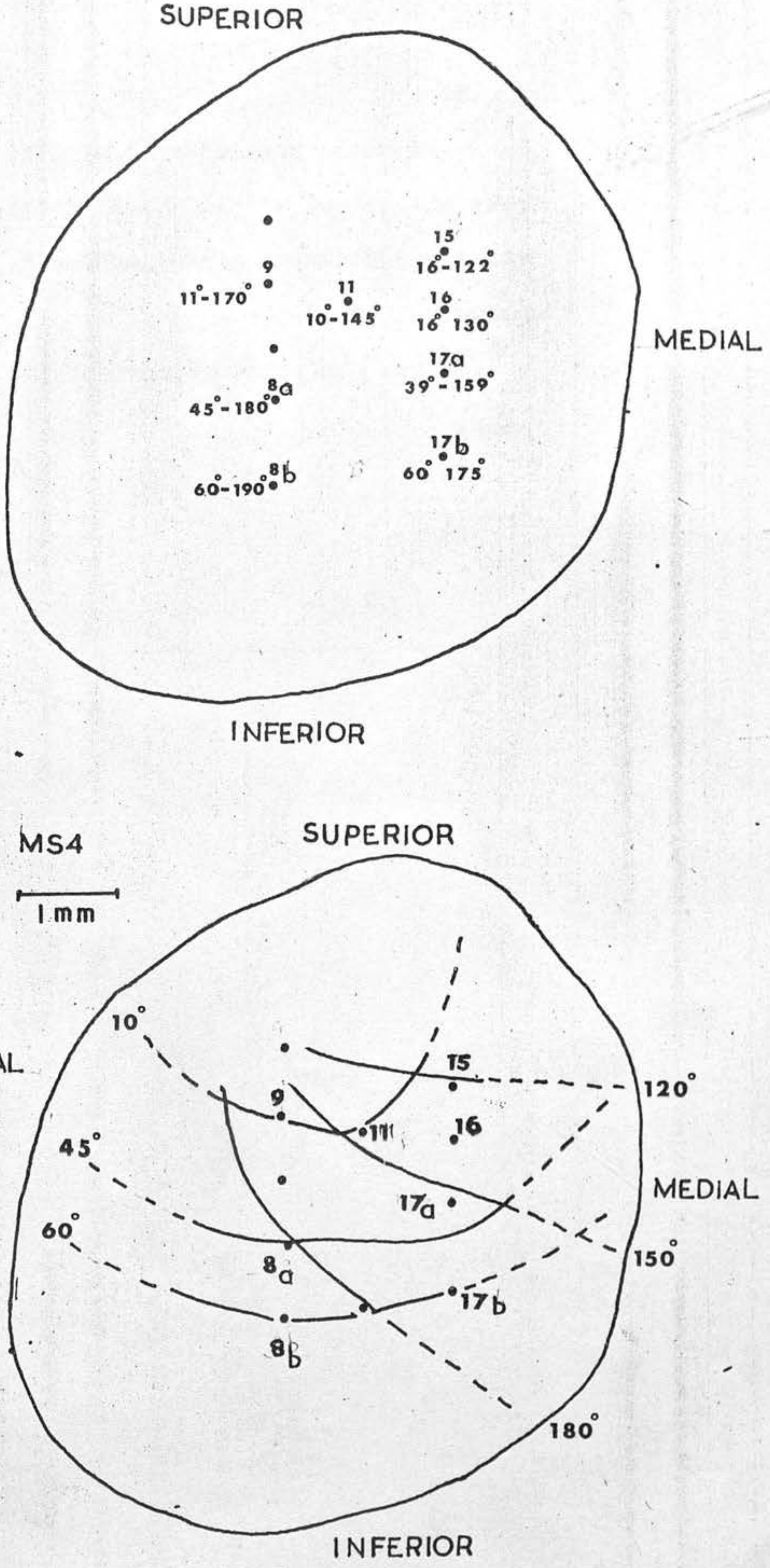
Plane projection of surface of superior colliculus, left.

Fig. 36

Projection of the visual hemi-field of the right eye on the left dorsal surface of the baboon's superior colliculus, plane projection. (MS4).



Baboon, visual hemi-field, right eye.

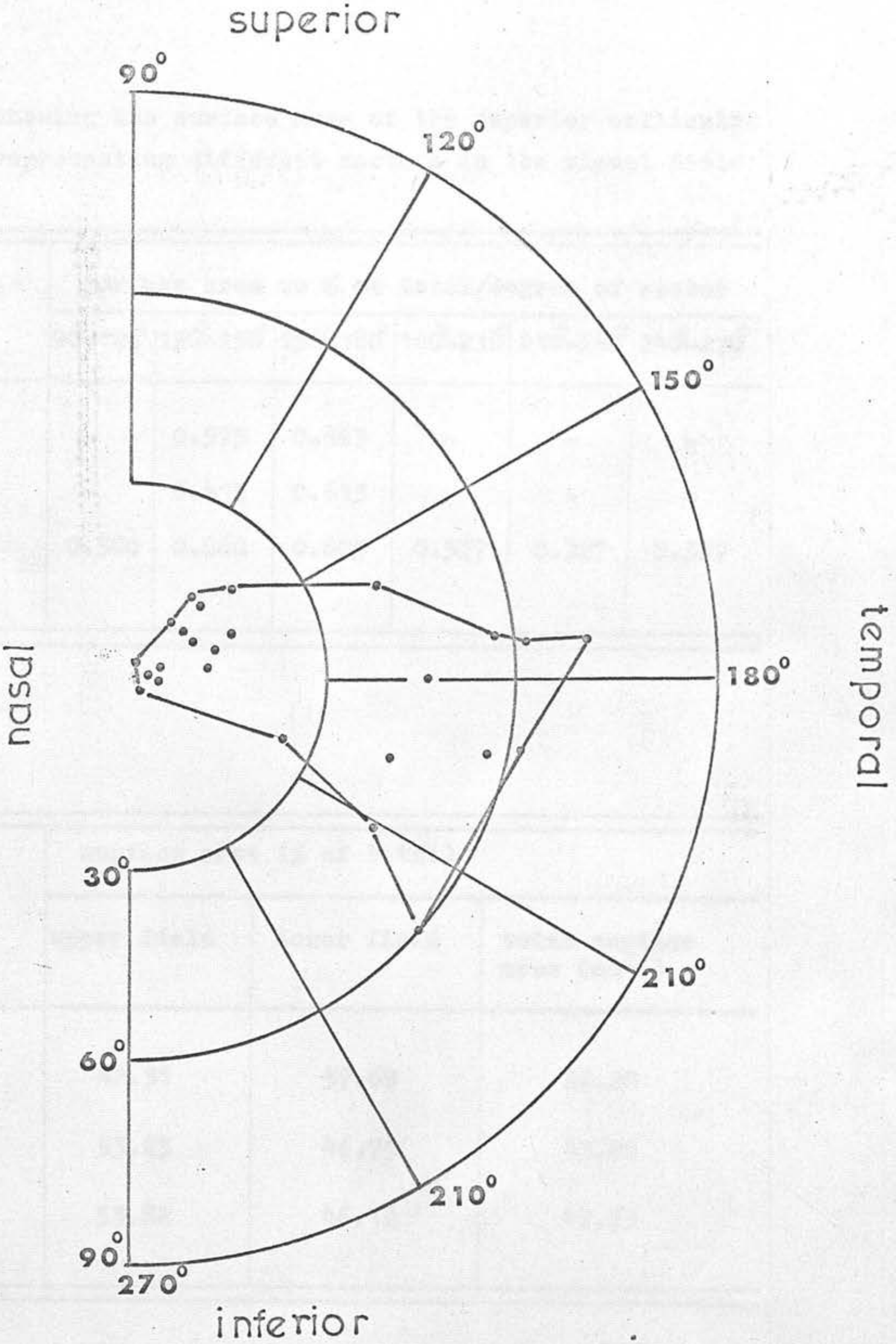


Plane projection of surface of superior colliculus, left.

Fig. 37

Composite results of 3 mapping experiments to illustrate the extent of the visual field subserving by baboon's superior colliculus as determined by electrophysiological method.

Note; the point represents the center of a receptive field.



Baboon, visual hemi field, right eye.

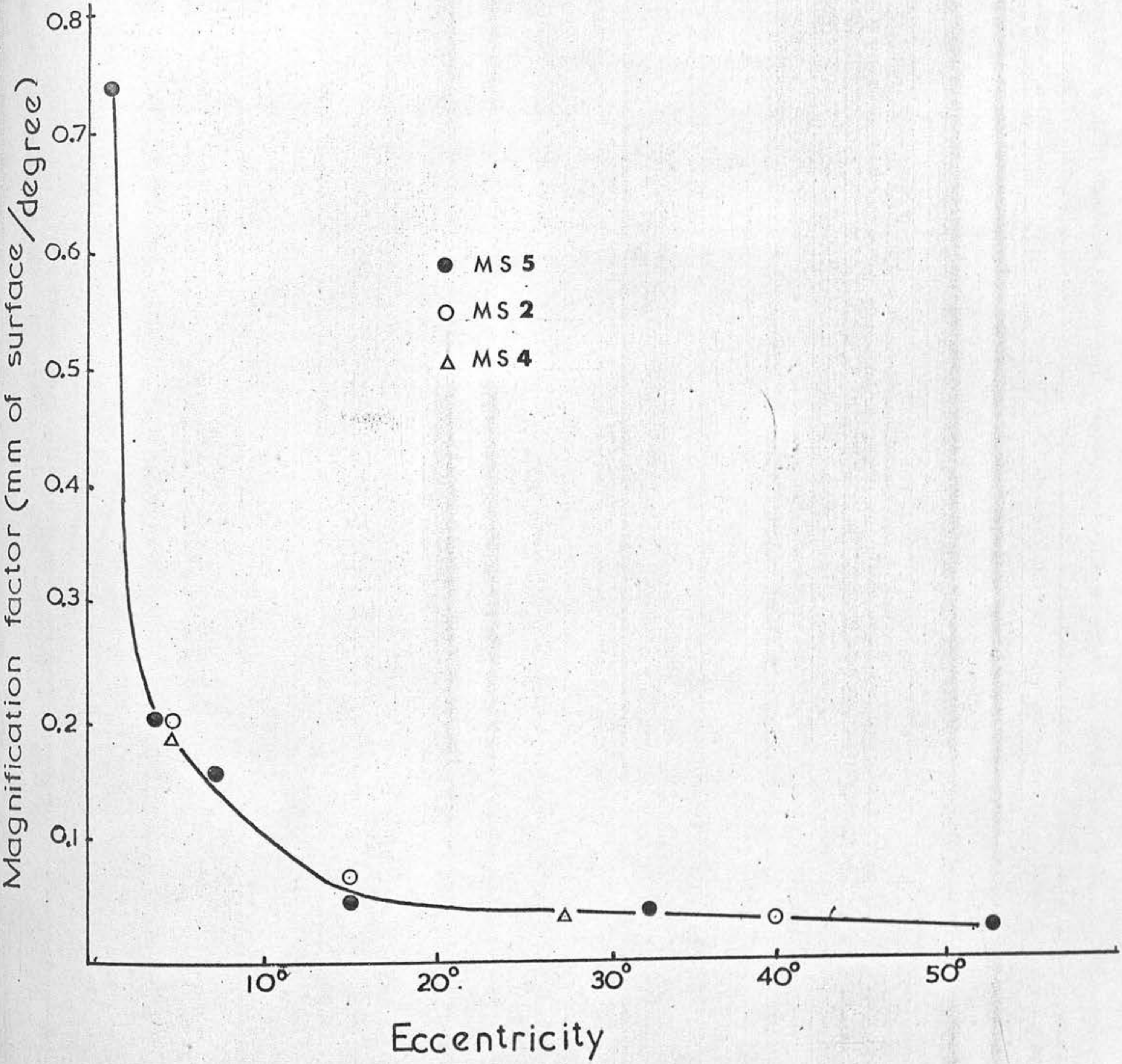
Table 5: showing the surface area of the superior colliculus representing different sectors in the visual field

Expt.	body wt. (kg.)	surface area as % of total/degree of sector					
		90°-120°	120°-150°	150°-180°	180°-210°	210°-240°	240°-270°
MS2	4.50	-	0.575	0.563	-	-	-
MS4	5.77	-	0.412	0.615	-	-	-
MS5	8.00	0.300	0.660	0.603	0.527	0.327	0.327

Expt.	body wt. (kg.)	surface area (% of total)		
		upper field	lower field	total surface area (mm^2.)
MS2	4.50	42.31	57.69	28.20
MS4	5.77	53.25	46.75	43.06
MS5	8.00	53.82	46.18	47.93

Fig. 38

Composite results of 3 experiments (MS5, MS2, and MS4), to show variation of magnification factors with retinal eccentricity along the horizontal meridian.



Magnification factor (mm of surface/degree)
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
● MS 5
○ MS 2
△ MS 4
10°
20°
30°
40°
50°
Eccentricity

Fig. 39

Composite curves to show the relationship of magnification factors of visual cortex (A), and superior colliculus (B), and centro-peripheral retinal ganglion cell density (C) along the horizontal meridian.

(A - reproduced from Daniel and Whitteridge, 1961; and C - from Whitteridge, personal communication.)

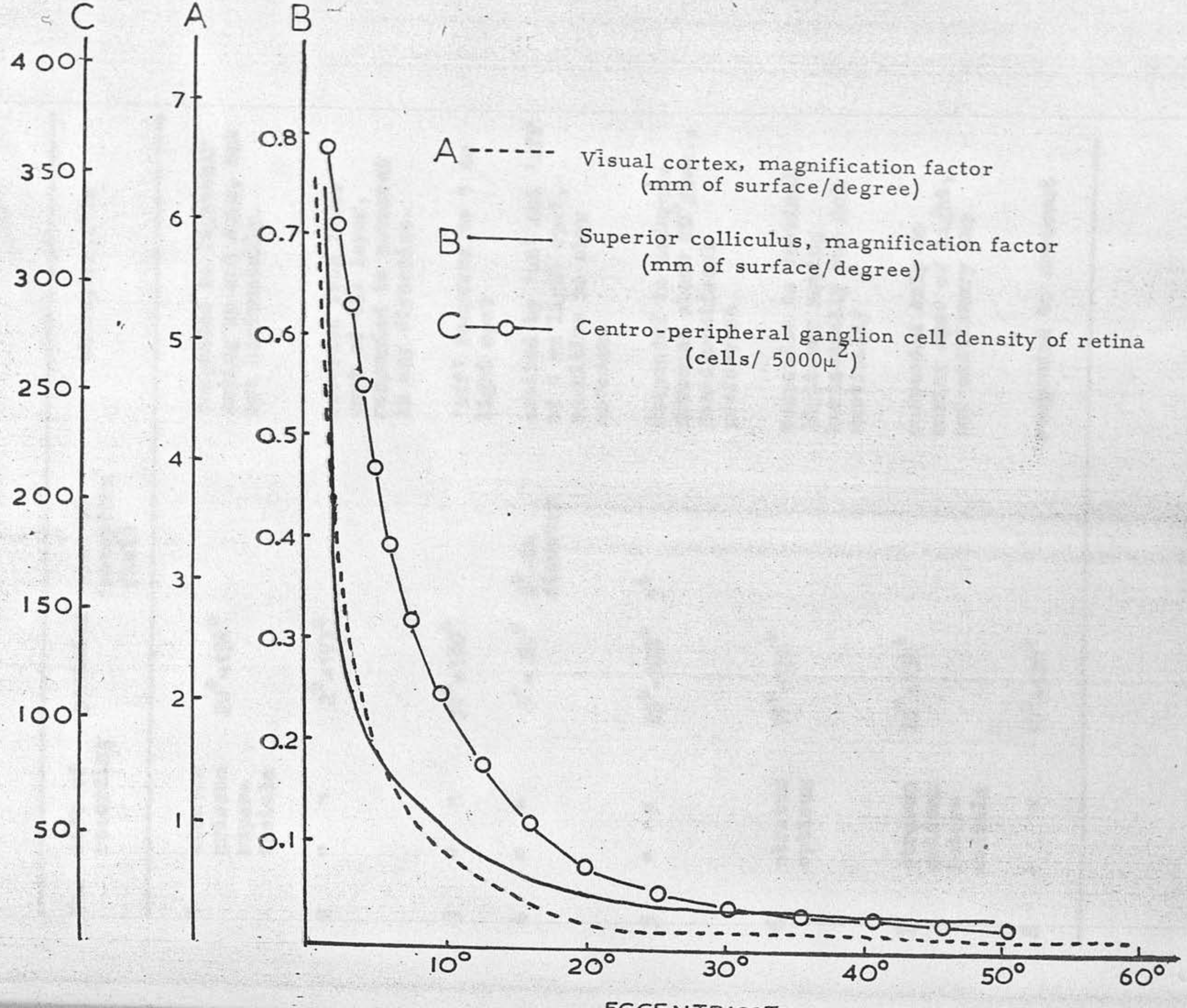

C
A
B
400
350
300
250
200
150
100
50
7
6
5
4
3
2
1
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
A - - - - - Visual cortex, magnification factor (mm of surface/degree)
B ——— Superior colliculus, magnification factor (mm of surface/degree)
C —○— Centro-peripheral ganglion cell density of retina (cells/ 5000μ²)
10°
20°
30°
40°
50°
60°
ECCENTRICITY

Table 6: units recorded from the superior colliculus of baboon.

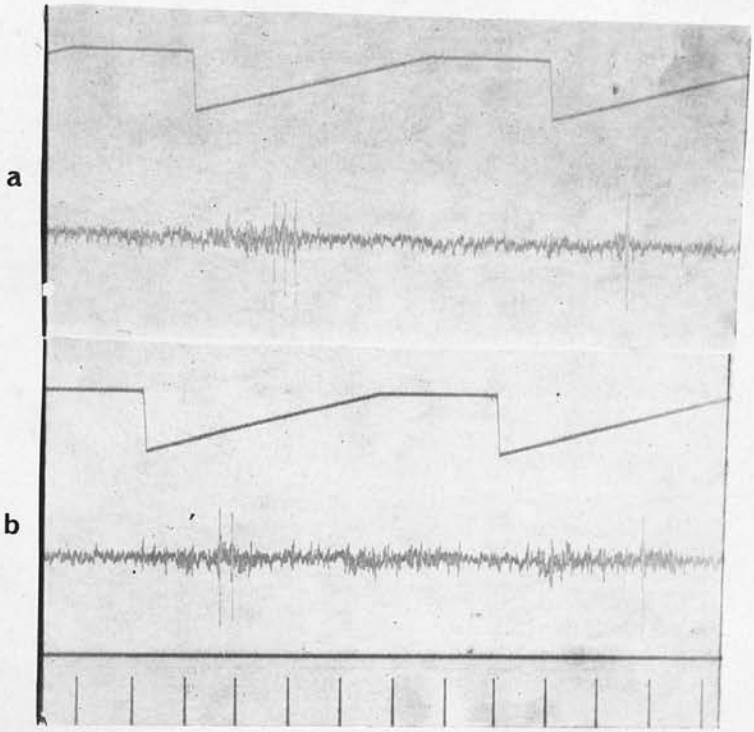
No.	site of recording	position	size of receptive field	characteristic
1	stratum griseum superficiale	20°-134°		responded to light-bar moving up and down, but not horizontally.
2	" "	2°-173°		recorded from lower part of the layer, respomded to movement in any direction.
3	" "	39°-180°		'off' response to 1 mm light spot
4	" "	3°- 20°	3° in diameter	excited by 'on' and 'off of 1 mm light spot, sensitive to slow movement
5	" "	25°-338°	5°	responded to moderate movement about 20°/sec., non-directional preference
6	stratum opticum	17°-156°		responded to vertical light-bar moving horizontally but not vertically
7	stratum griseum intermediale	20°-134°		responded only to moving spot of light, not stationary one.
8	" "	10°-120°		responded to movement

Fig. 40

(a) Unit responded to a rectangular light bar about 10° wide and 2° thick moving horizontally, but not vertically across the receptive field. This unit was recorded from the stratum opticum and had a receptive field center at 17°-156°. The upper trace in the record shows the signal of a moving stimulus (MS2).

(b) Another specific orientation unit, recorded from the stratum griseum superficiale, had a receptive field center at 20°-134°. The optimum stimulus was a light bar moving in a vertical direction back and forth across the receptive field, no responses in the other directions. (MS2)

Time in each record 100 msec.


a
b

THE CEREBELLAR VISUAL AREA OF THE CAT

IV. THE CEREBELLAR VISUAL AREA OF THE CAT

Out of 24 cats in this study, good visual responses at unit level were achieved in about half of the preparations. In some preparations, the visual responses could not be elicited from the cerebellar cortex but could be elicited from the visual cortex. Difficulty in obtaining the visual responses from the cerebellar visual area has been noted by previous authors (Snider and Stowell, 1944; Henneman, Cooke, and Snider, 1952; and Fadiga, Pupilli, and Berger, 1957) who have pointed out the extreme sensitivity of the cerebellar cortex to circulatory changes and the lability of the visual responses. In some preparations, good auditory responses were obtained but visual responses could not be elicited by any means. In some parts of the cerebellar visual area, the visual responses could not be evoked in spite of the occurrence of spontaneous activity.

Moving stimuli and neon flashes were used to elicit visual responses in the cerebellar visual area. The behaviour of the latter type of stimulus was an interesting problem. The visual response occurred only after the presentation of a neon flash at the perimeter arm for the first time. It consisted of a sharp biphasic wave with a brief burst of spikes superimposed. If the stimulus was presented in the same place and within a short interval, no response was elicited again. On the contrary, if the neon stimulus was moving around by changing the place of stimulation, the visual responses could be obtained nearly every time. In this case, the localization of the receptive field could not be found. The responses could be elicited all over the more central part of the visual field within about some 45° from the center of fixation. On the other hand, one could locate the position of the receptive field by using a moving stimulus. It seemed that the visual responses evoked by the neon flash were the movement effects of light.

A. THE EXTENT OF THE CEREBELLAR VISUAL AREA

The extent of the cerebellar visual area was determined by moving stimuli. The boundary of the whole cerebellar visual area could not be determined in any single experiment, because some parts of the expected visual area were free of visual responses during the penetration of an electrode. The extent of the visual area presented here was obtained from the observations of a number of experiments. The visual area confined to the declive (lobule VI), and folium-tuber vermis (lobule VII.). No visual responses were found in the neighbouring areas of the lobules VI, and VII, namely the paramedian lobules, crus I and II, and anterior lobe. In Fig. 42a, three electrode tracks have been shown to penetrate the cerebellar visual area. The most anterior electrode track (on the right side of the figure) after recording the visual responses from 4 folia, entered the anterior lobe from which the spontaneous units without visual evoked responses were obtained. Auditory responses were also observed, but no attempts were made to investigate these responses systematically.

The extent of the visual area in the present study is, in general, in agreement with the cerebellar visual area described by Snider and Stowell (1944), and Fadiga, Pupilli, and Berger (1957), who found the maximal visual response in the region of the tuber-vermis. However, their response also included the neighbouring structures, e.g., covering the primary fissure to invade the two or three most caudal folia of the culmen, rostral folia of the pyramis, and medial portions of the paramedian lobule. Furthermore, with very strong stimuli the visual responses could be elicited from the whole cerebellar hemisphere as well as the vermian portion (Fadiga, Pupilli and Berger, 1957). It is certain that the very strong stimuli and much less selective electrodes used by these investigators were the cause of the larger visual responsive area. In addition, the silent areas separated by the area of maximal responses as described by Snider and Stowell (1944) have not been observed in the present experiments.

Several attempts have been made to elucidate the problem of retinotopic organization onto the cerebellar visual area. The retinotopic organization, however, so far has not been accomplished. Whether there is no proper retinotopic projection or the projection patterns are complicated or distorted by the complexity of the folia's patterns must be determined in the future.

B. SINGLE UNIT ACTIVITY IN THE CEREBELLAR VISUAL AREA

The visual responses of 104 units recorded in the cerebellar visual area have been studied. One characteristic which was common to all units was the habituation to repeated stimuli. If the successive stimuli, the moving stimuli used in the present study, were applied with an interval of less than 1 sec., usually no responses could be elicited but the responses occurred after the time lapse of a few seconds or more, and after about 5 sec. strong responses could be evoked. Another way of exciting a unit after its responses to a stimulus had waned was to shift the position of the stimulus in the receptive field.

The latencies of the visual stimuli either by a moving light-bar or a neon flash placed at the perimeter arm were measured from a small sample of units and latencies of about 40-50 msec. were obtained (Fig. 44, a, b, c.). The spontaneous resting discharges have been observed frequently, but the majority of them were non-visual units. Two types of spontaneous firing units, the rhythmic bursts of spikes and units firing at a regular interval were observed (Fig. 44, d and e). The discharge frequency of the latter type was about 60/sec. Brookhart, Moruzzi, and Snider (1950) studied the spike discharges of single units in the cerebellar cortex and found that the rate of single unit discharge was generally in the range of 70 to 80/sec., but, however, lower frequencies (about 30/sec.) as well as higher (150-160/sec.) were also recorded in the decerebrate preparation.

The units in the majority of cases could be stimulated with either eye and the same directional preferences were obtained, from both eyes. The opposite preferred directions have not been observed. Surprisingly, some units required binocular stimulation, occlusion of either eye resulting in no response at all in spite of strong stimulation. However, in some units, monocular stimulation gave a weaker response than the binocular one.

I. Non-directionally selective unit

Medium sized receptive field unit

Seventeen units, consisting of 16.35% of the total population, have been observed in this series. The size of the receptive field, measured by a moving stimulus, varied between 10°-20° in diameter. Since there was no response to a stationary light stimulus and only fast movement could elicit the response, the boundary of the receptive field unit could not be measured with accuracy, only an approximate boundary being obtained. No directional preferences were detected in this kind of unit. The behaviour of units is shown in Fig. 43B. The units showed a response to fast movement across the receptive field within a certain range of velocity but the optimum speed varied from 100°-300°/sec. The size of the stimulus was not a critical factor, a 2° wide stimulus could be as effective as a 10°. In some cases, the stimulus size larger than the receptive field gave less response than a small one.

The distribution of this kind of unit and the directionally selective units which will be mentioned later on, has been observed , and the centers of the receptive fields were found to scatter around the center of the visual field, being at 5°-40° from the center of fixation.

Large receptive field unit

This type of unit, consisting of 22 units, (21.15% of the totalsample), had characteristics which were different from the other 3 groups (Fig. 43A). First, the receptive field was larger, being about 30°-60° across and covered the central region of the visual field. Secondly, the optimum velocity, being about 50-100°/sec., was slower than the other 3 groups. However, the units showed responses to a wide range of velocity. Although the units had a very large receptive field, a small stimulus as small as 2-3° wide, and very small excursion of movement could elicit the response all over the field. Thirdly, this large receptive field unit showed less habituation to repeated stimuli. The visual response could be evoked by repeated stimulation at a short interval.

2. Directionally selective unit

Centrifugal unit

This group of units is an interesting one, because it showed the response to movement in a selective direction. 36 units have, so far, been observed. The units showed the behaviour in common that a fast movement about 100°-400°/sec. moving across the receptive field in a centrifugal direction (moving away from the center of the visual field), was an optimum stimulus. No responses could be elicited in a centripetal direction. However, the range of the directional response seemed to vary from unit to unit. (Fig. 49). The receptive field as measured by such moving stimuli was approximately 10°-20° in diameter. Some units showed a receptive field smaller than 10°. The behaviour of this kind of unit is illustrated in Fig. 43C, 45 and 46, and their distribution in the visual field, including the range of directional responses, is shown in Fig. 49. One of the characteristics which is worth mentioning, is that movement in a centrifugal direction not only evoked no response, but also seemed to inhibit the resting discharge in some units (Fig. 46, 48b).

Uncategorized group

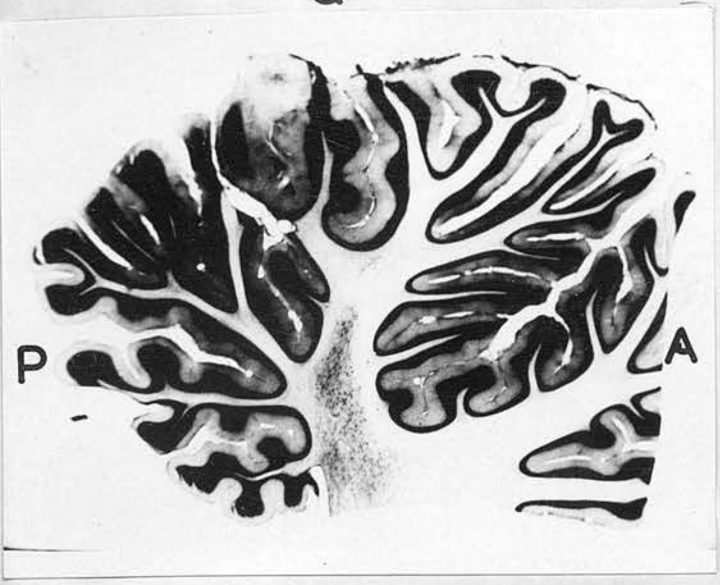
A number of units recorded in this series of the present study showed variable responses to moving stimuli, which could not be classified into either a non-directional medium-sized receptive field unit or a centrifugal unit. This kind of unit showed variation in response to moving stimuli from time to time, but after the observations were made repeatedly the optimum stimulus of such units was revealed. Movements in both centrifugal and centripetal directions were the optimum stimuli in one group of units, but not in a perpendicular direction (Fig. 43D and 47). Some units showed the responses to movement in every direction, but after repeated observations, it seemed that movement in a centrifugal direction still gave more responses than other directions (Fig. 43 E and 48 d).

Fig. 41

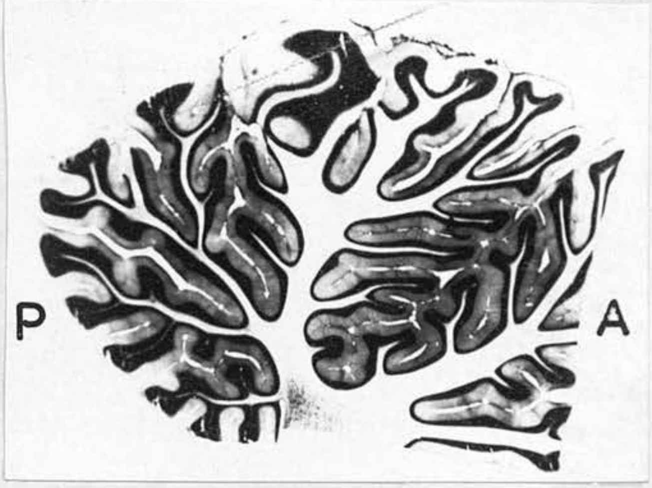
Serial parasagittal sections at the region of tuber-vermis to show the different patterns of folia resulting from the turns of vermis. (CC23).

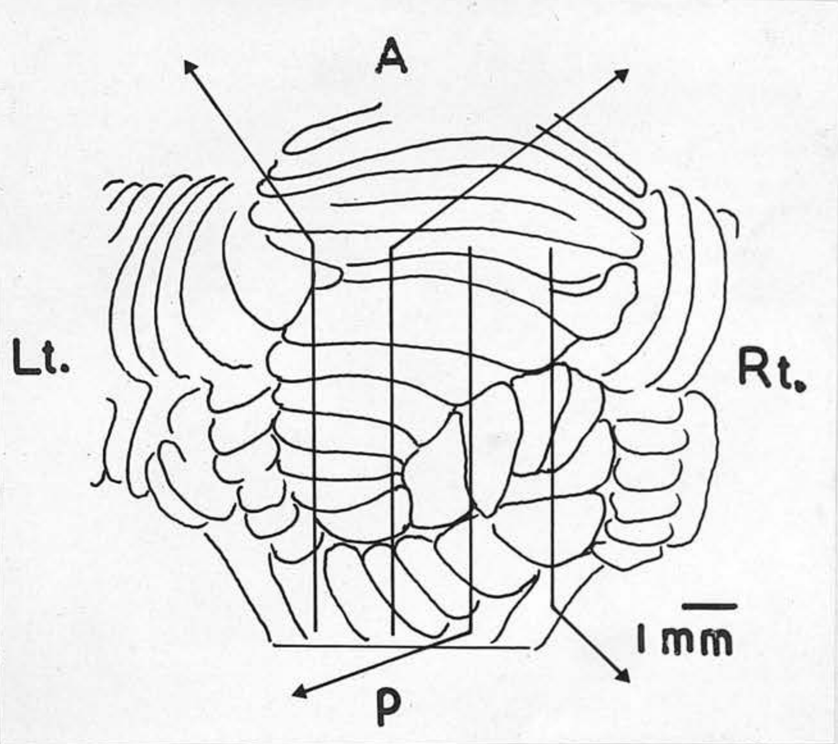
Section magnification of a, b, c, and d are 5.7, 5.4 5.7, and 6.0 times respectively.

a



b





c

d

Fig. 42

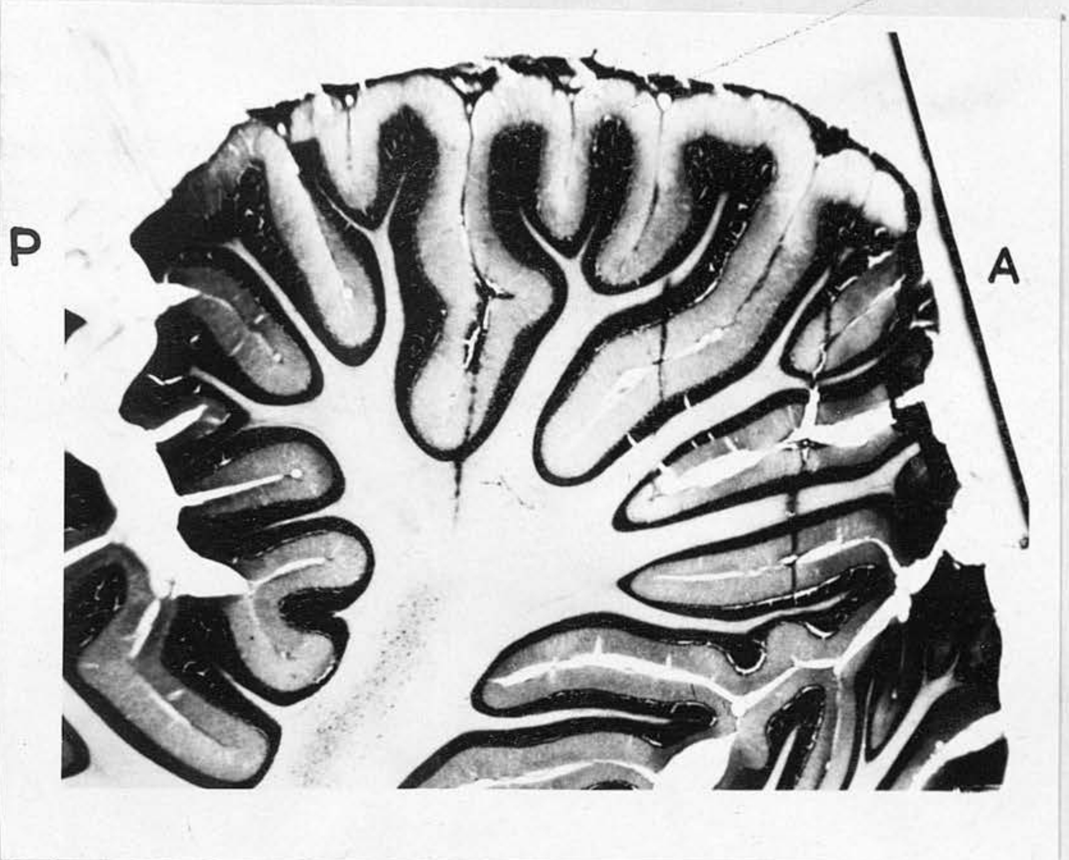
(a) Photomicrograph of a parasagittal section of cat's cerebellum to show the course of 3 electrode tracks. (CC20).

Section magnification x 11

(b) Parasagittal section of cat's cerebellum at the region of vermis to show 3 electrolytic lesions, indicated by arrows. (CC23).

Section magnification x 12.

a



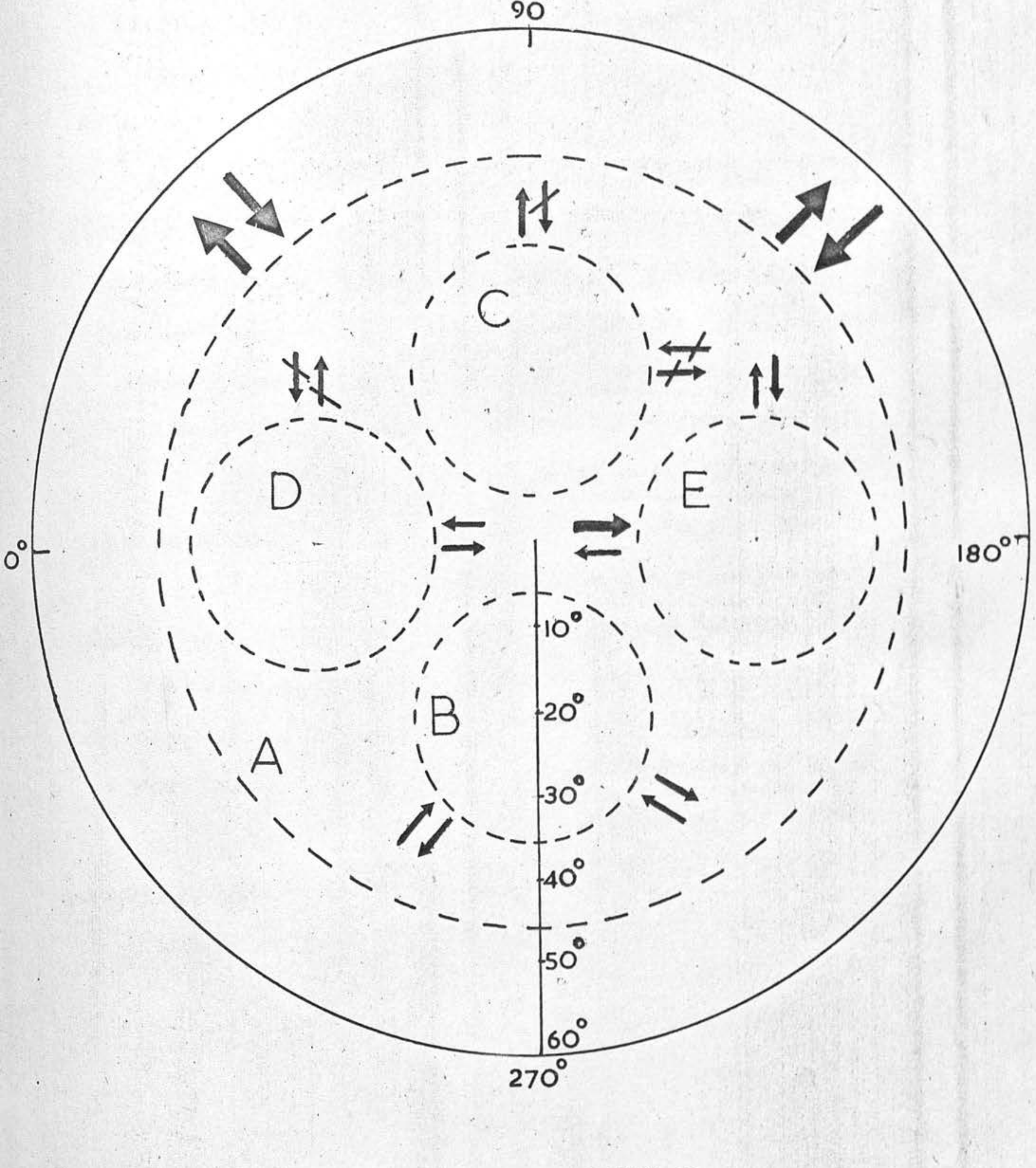
b

Table 7: classification of units recorded from the cerebellar visual area.

Unit type	size of receptive field	Optimum stimulus	Nos.	%
1. Non-directionally selective unit.				
A. medium receptive field unit	10°-20°	moderate to fast movement in any direction, 100°-300°/sec.	17	16.35
B. Large receptive field unit	30°-60°	moderate movement in any direction, 50°-100°/sec.	22	21.15
2. Directionally selective unit				
A. centrifugal unit.	10°-20°	fast movement in a centrifugal direction, 100°-400°/sec.	36	34.61
B. Uncategorized	10°-20°	moderate to fast movement with directional preference.	29	27.87

Fig. 43

Diagram showing the different sizes of the receptive fields and their behaviour in responding to moving stimuli. Broken line represents a boundary of the receptive field, and an arrow indicates the direction of movement of stimuli. The sizes and positions of the receptive fields in relation to the visual field are shown.



CAT, VISUAL FIELD.

Fig. 44

The upper records (a, b, and c) show the latencies of the visual responses.

(a) Response from a light-bar moving across the receptive field at the rate of 360°/sec. Two photocells, placed 10° apart, were used to measure the velocity of the stimulus. The latency in this case is 41.7 msec. Time, 100 msec. (CC16).

(b) and (c), responses from a neon light, at the perimeter arm (33 cm from the eye), with the latencies 44.02 and 50.0 msec respectively. Time 10 msec in each case. (cc22).

(d) shows rhythmic bursts of spikes of non-visual spontaneously firing units. Time, 10 msec. (CC18).

(e) shows another type of spontaneously non-visual unit, frequency about 60 / sec. Time 10 msec. (CC23).

(f)Brief response to movement with high frequency spikes over a large region of the central visual field, about 40° across. Rate of movement about 50°- 100°/sec. The responses could be elicited by movement in every direction, and even a short distance. (2°-3°). (CC22).

(g) Another type of large field unit response to movement with low frequency discharge in the central region about 40° across. (CC20).

Time in both records, 10 msec.

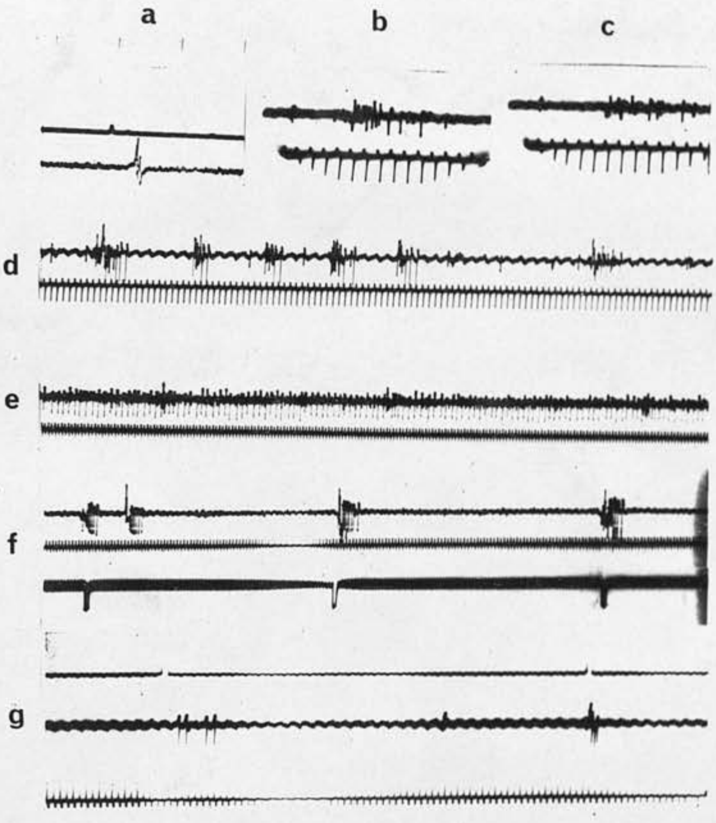

a
b
c
d
e
f
g

Fig. 45

Responses of a centrifugal unit to fast movement in different directions. This unit was on 25°-120° and had a receptive field size about 10° in diameter, indicated by a broken circle. The small arrow indicates approximately when the light-bar entered the receptive field, and the large arrow shows the direction of the stimulus, being about 2° x 10° in size, and having a velocity of about 300°/sec. Time, 10 msec. (CC22).

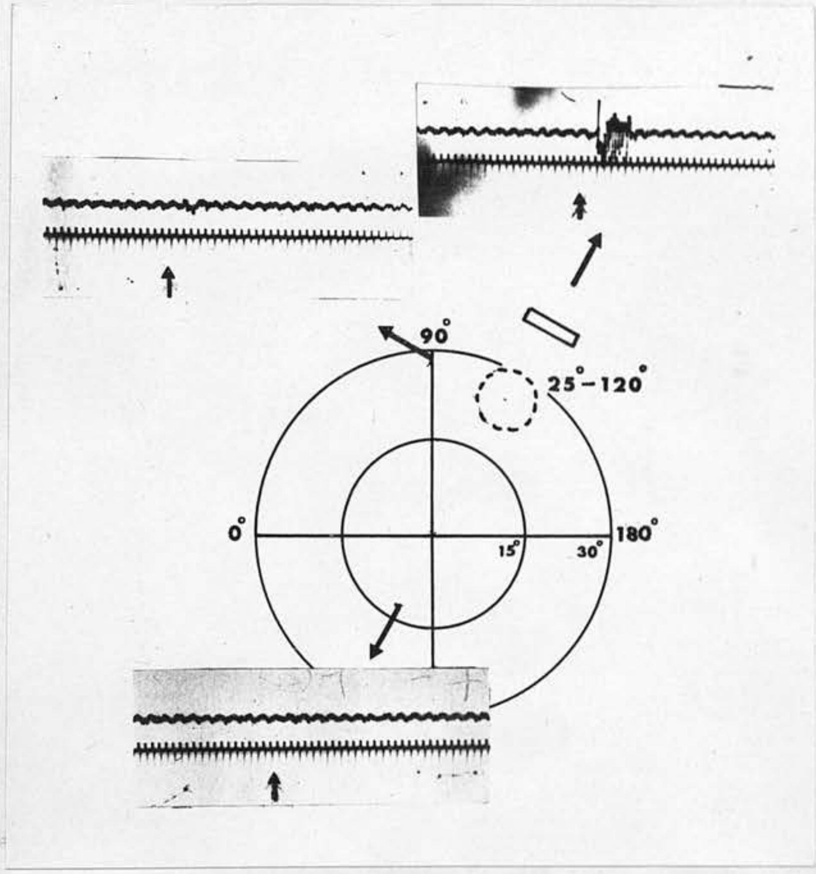

90°
25°-120°
0°
180°
15°
30°

Fig. 46

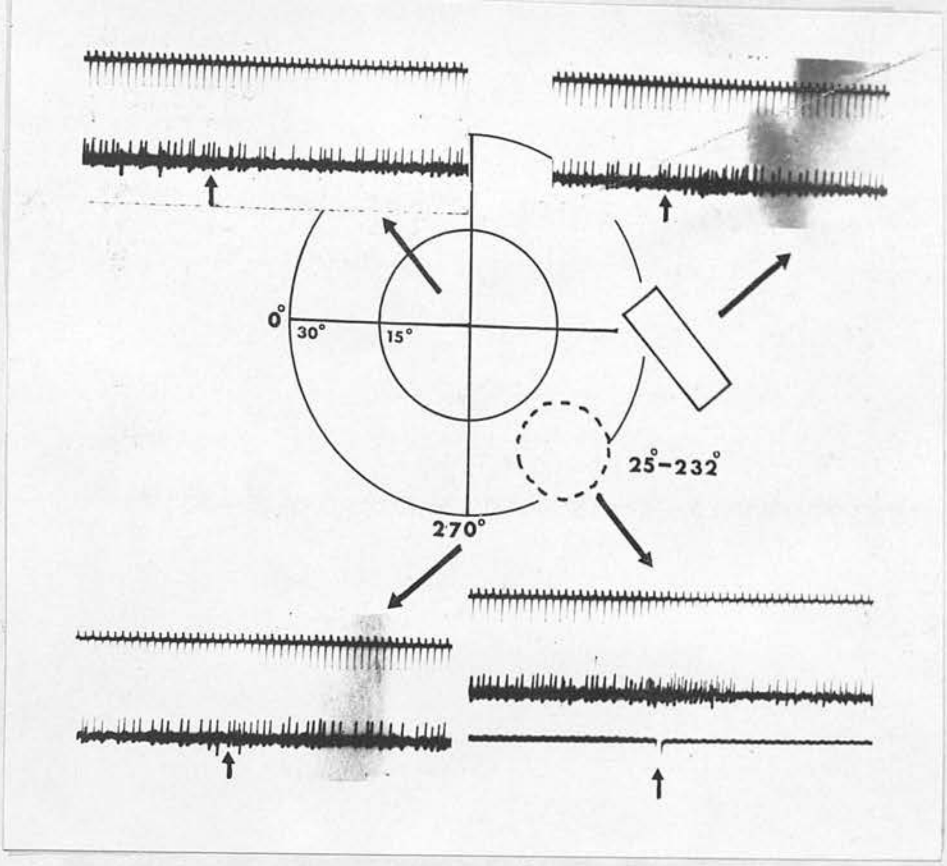
Responses of another centrifugal unit to fast movement in various directions. A receptive field was 25° from the center on the radius 232°, and had a receptive field size approximately 15° in diameter. The stimulus was a light-bar 7° x 20° in size, with a velocity of about 250°/sec.
Time, 10 msec. Symbols as in Fig. 45. (CC22).

Fig. 47

Responses of a directionally selective unit, positioned on 23°-238°, to a rectangular light-bar, moving back and forth across the receptive field in the centrifugal, centripetal and perpendicular directions. A large arrow indicates the direction of movement (downward- centrifugal and upward- centripetal), and a small arrow indicates an entering point of the stimulus into a receptive field. Rate of movement about 250°-350°/sec.
Time, 10 msec. (CC22).

Note the variability of the responses. All records read from left to right.

46



47

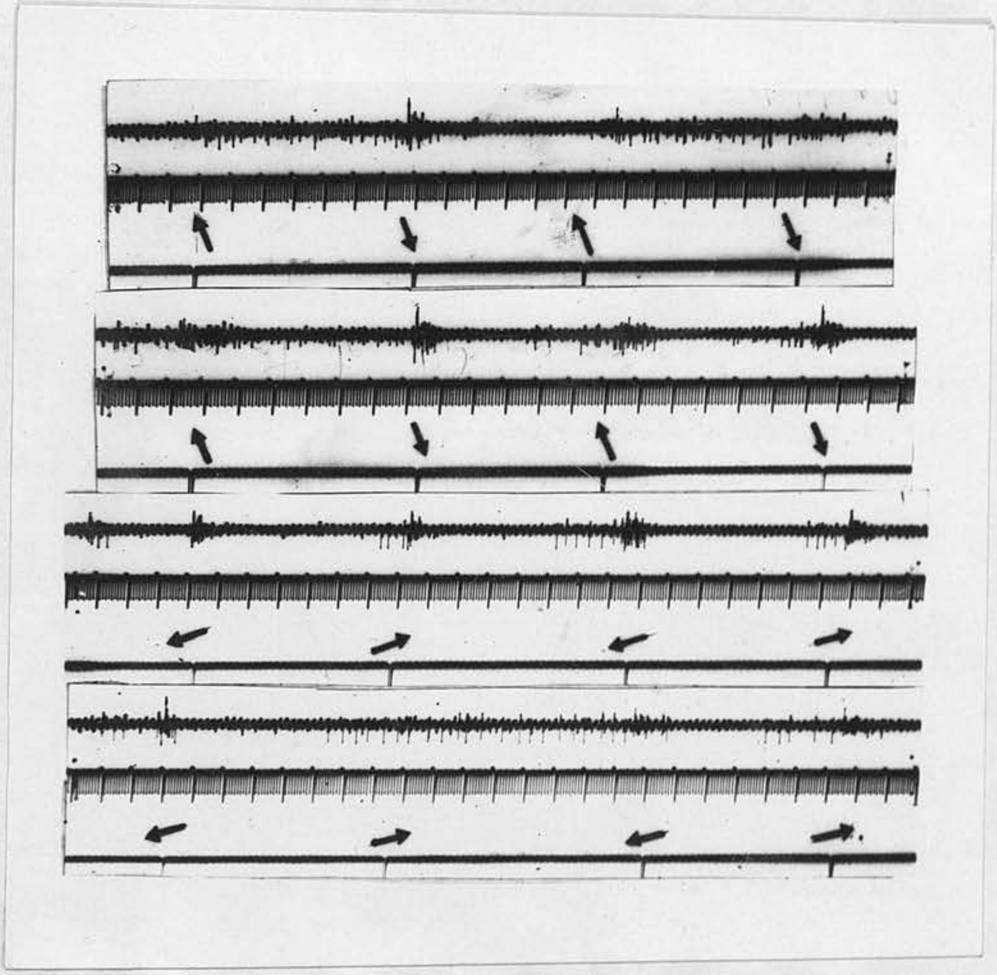


Fig. 48

(a) Responses of a medium receptive field unit to fast movement (about 200-300°/sec) in different directions. The stimulus was 10° wide, 2° thick light-bar. The large arrow indicates the direction of motion, whereas the small arrow represents an approximate point of a stimulus entering the receptive field. Time in each record, 10 msec.(CC17).

All records read from right to left.

(b) Responses of a unit to fast movement (about 200° - 350°/sec) in a centrifugal direction (left). Note the inhibition of the resting discharge by the centripetal movement (right). (CC22).

(c) Shows two unit responses being recorded from the same electrode position. The small unit responded to the stimulus moving in both centrifugal and centripetal directions, while the large unit responded only to centrifugal movement (left). Stimulus size 7° x 20°, and rate of movement about 300°/sec. Approximate position of receptive field, 15° from the center, and on the radius 15°(CC22).

(d) Responses of another directionally selective unit to movement of a rectangular light-bar back and forth across the receptive field in the centrifugal (left) and centripetal (right) directions. For the testing stimuli in each direction, 3 out of 10 could be elicited in centripetal direction, but every time in centrifugal direction. In other directions no responses could be elicited. (CC22).

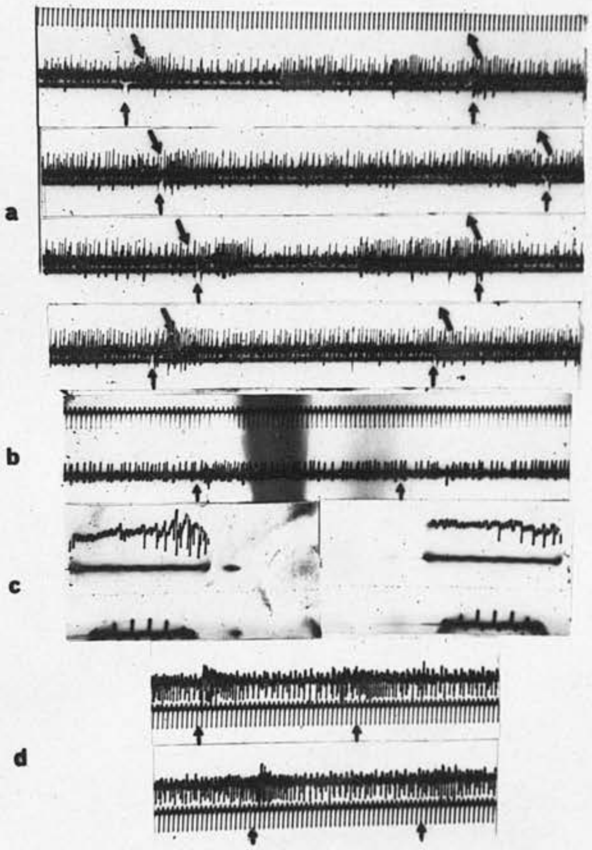
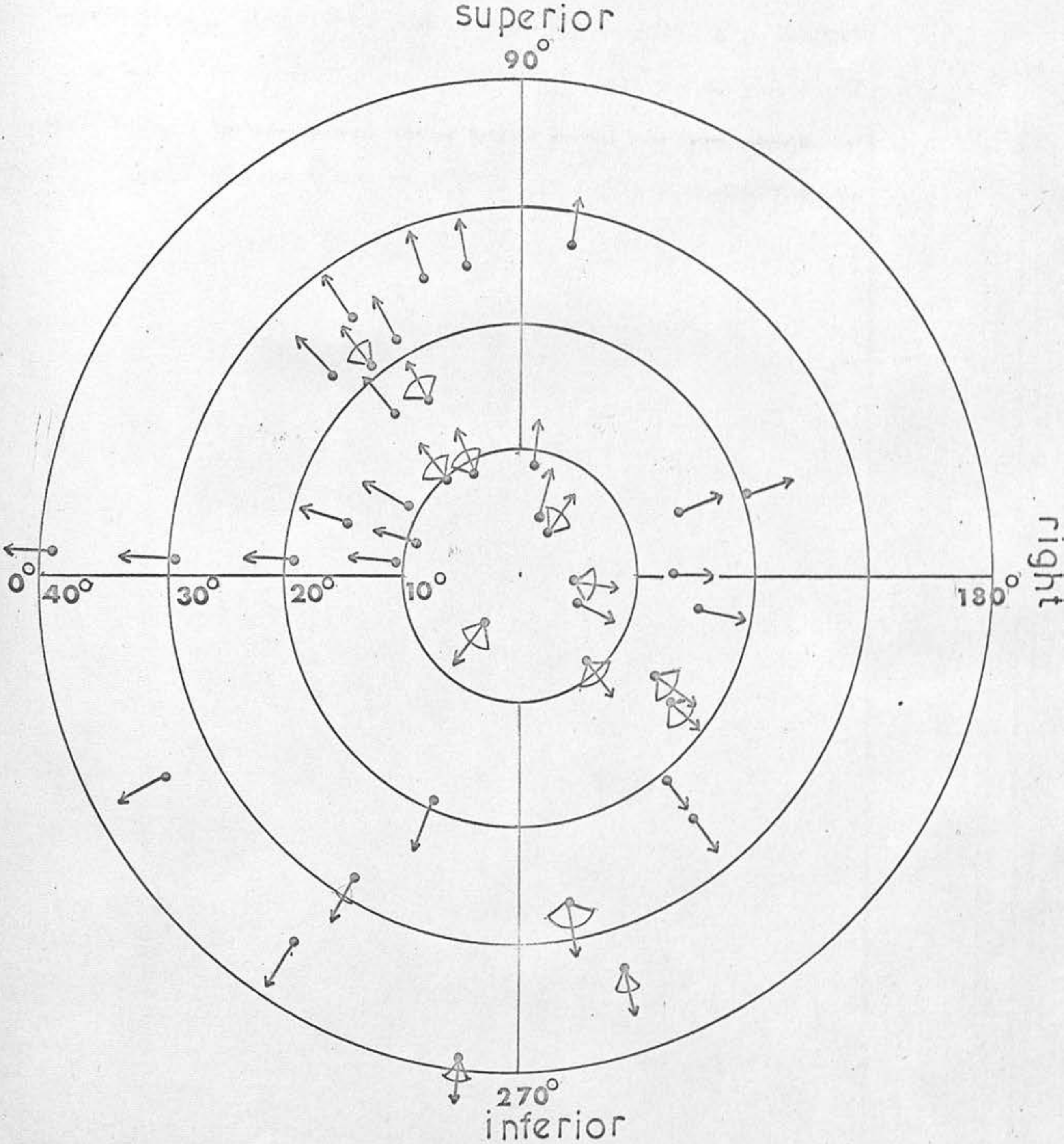

a
b
c
d

Fig. 49

Distribution of the receptive field centers of 35 centrifugal units recorded from the cerebellar visual area. The arrow indicates the direction of movement of optimum stimulus, and the acute angle shows the range of directions of movement in which the responses could be elicited.



Cat, visual field.

DISCUSSION

NUCLEUS INTERLAMINALIS MEDIALIS OF L.G.N.

I. NUCLEUS INTERLAMINALIS MEDIALIS OF L.G.N.

A. RETINOTOPIC ORGANIZATION

The organization along a rostro-caudal axis, with the lower visual field projecting to the anterior part of the nucleus, and upper visual field to the posterior part of the nucleus in the present experiment is in agreement with the anatomical studies (Garey, 1965; Laties and Sprague, 1966; and Stone and Hansen, 1966). In the case of Stone and Hansen (1966) they have found clear evidence of the retinotopic organization in antero-posterior direction only in the ipsilateral N.I.M. not in the contralateral N.I.M.

The present experiments also show some degree of retinotopic organization in a dorsal-ventral direction as well as a medio-lateral direction. There are controversial views of the retinotopic organization among anatomical studies by various authors. In a preliminary report by Garey (1965), he describes "the central area is represented in the more dorsal part of the nucleus, while peripheral lesions cause degeneration in the ventral half".

Stone and Hansen (1966) found some medio-lateral organization of ipsilateral and contralateral projections. Degeneration either in the medial or lateral edge of the N.I.M. resulted from lesions in the contralateral eye whereas in the ipsilateral eye it was usually situated approximately centrally. Their findings are consistent with Hayhow's descriptions (1958) of three vertically orientated layers, the middle layer having ipsilateral afferents, the medial and lateral layers having contralateral afferents. The present result did not reveal this organization. Most of the responses were obtained from the contralateral eye, only a few of them were from the ipsilateral eye.

Laties and Sprague (1966) described degeneration in the N.I.M. after lesions of both central and peripheral retina; in contrast to Stone and Hansen (1966), who found degeneration only from the peripheral and pericentral areas, not from the central area. This had led the latter authors to suggest that "the N.I.M. does not take part in the pathway directly involved with visual perception, but serves some accessory function". The present study, in this aspect, is in agreement with Stone and Hansen (1966) in which no responses were obtained from the central retina.

The extent of the visual field in the present study has been found up to 60° or 70° from the center of fixation, whereas Bishop (1965), by electrophysiological method, found only the more central parts of the visual field.

B. EFFERENT CONNECTIONS FROM THE NUCLEUS INTERLAMINALIS MEDIALIS

In order to understand the function of this nucleus, it is necessary, as a first step, to know the connections of this nucleus. Garey (1965) has reported retrograde degeneration on the N.I.M. following cortical lesions placed lateral to the area 17. His results suggested that cellular degeneration in the N.I.M. is found when the lesions extend beyond area 17, but whether area 18, 19 or both is the termination has not been determined.

Wilson (1966) has tried to clarify this problem; his technique was to make electrolytic lesions in the N.I.M. stereotaxically, using a horizontal approach to avoid damage to the corpus callosum. However, lesions which include the N.I.M. produced degeneration in the visual area III in the bottom of the splenial sulcus and on the middle suprasylvian gyrus. His relevant lesions always involved the N.I.M., but also extended in to the adjacent parts of the pulvinar nucleus. One medially placed lesion was restricted to the pulvinar, lateral posterior nucleus, and the middle suprasylvian gyrus is the only part of the cortex which shows degeneration.

In addition to the main ipsilateral cortical projection from the N.I.M. Bishop (1965) has cited the evidence for a contralateral cortical projection from the N.I.M. made by Hansen in his laboratory; there was evidence of degeneration in the opposite N.I.M., at least in one instance, following a lesion of the posterior part of area 17 on the medial surface of the hemisphere, via corpus callosum. Contralateral degeneration was only found following lesions at the medial surface of the hemisphere; the main nucleus was free of degeneration.

The functional significance of the double representation in the L.G.N. is not known. Bishop (1965) has suggested the role of the N.I.M. as a phenomenon analogous to macular sparing in man by the existence of contralateral cortical projection and by the retinal representation existing only in the more central region. On the other hand, Stone and Hansen (1966) could not find the representation in the N.I.M. after a central retinal lesion and this is in agreement with the electrophysiological mapping of the present experiments. Thus it is difficult to consider this as a possible function.

SUPERIOR COLLICULUS OF THE CAT

III. THE SUPERIOR COLLICULUS OF THE CAT

A. THE RETINAL REPRESENTATION ON THE SUPERIOR COLLICULUS

1. The retinotopic organization onto the superior colliculus

Since Apter has described the retinotopic projection onto the cat's superior colliculus in 1945 by electrophysiological methods, using moist wick electrodes, many investigators with more refined techniques using microelectrodes of different kinds and appropriate stimuli, have mapped the retinal representation onto the surface of the S.C. of mammals and optic tectum of lower vertebrates. Among the mammals are the rabbit - first mapped out by Hamdi and Whitteridge (1953) and continued by Seneviratne (1963); the rat - more recently by Siminoff, Schwassmann, and Kruger (1966); and Forrester and Lal (1966). Data on lower vertebrates are available for the pigeon - Hamdi and Whitteridge (1954); frog - Gaze (1958), and Jacobson (1962).

In addition, detailed retinotopic representation on the cat's visual centers has been shown recently; in the L.G.N. (Seneviratne and Whitteridge, 1962; Bishop, Kosak, Levick, and Vakkur, 1962, and Seneviratne, 1963), and in the visual cortex (Bilge, Bingle, Seneviratne, and Whitteridge, 1967; who have extended the works of Talbot, 1940, 1942).

A more accurate study of a projection of the retina onto the S.C. is of interest to compare either the collicular pattern of projection with that of the geniculostriate system in the cat itself, or with the collicular pattern of other mammals for the purpose of comparative studies.

The present study has described the retinotopic projection onto the flattened surface of the S.C., which is reconstructed from the serial histological sections. In general, these results have confirmed the work of Apter, that the anterior pole of the S.C. which is devoted to the central area of the retina seems to have a larger area than the rest of the retina. The horizontal meridian runs backward and slightly medially splitting the S.C. into the lateral part for the lower visual field, and the medial part for the upper visual field. The vertical meridian runs along the anterior edge of the S.C. The present results also have extended the information further. The area of the S.C. devoted to the lower field quadrant is larger than the upper field quadrant; this seems to be equal in the Apter chart. The difference can be explained at least for one reason, that the present maps were obtained from the surface of the S.C. which had been flattened out, and by the fact that the S.C. is curved in the lateral part more than the medial part. The disparity between the areas devoted to the representation of the lower and upper field quadrants has also been shown to exist at the geniculate level as described by Seneviratne and Whitteridge (1962), and in the visual cortex (Bilge, Seneviratne, and Whitteridge, 1963), and more recently by Bilge, Bingle, Seneviratne and Whitteridge (1967). The ratio of the areas between the lower and upper field quadrants in the L.G.N. as measured by these authors is 2:1. The ratio of 1.38:1 is obtained in the S.C. from the present experiments.

The retinal ganglion cell studies (Stone, 1965) do not reflect the disparity of the surface areas of either the geniculostriate center or the collicular center, devoted to the representation of the upper and lower field quadrants. Instead, they show equal distribution along both the upper and lower fields.

Seneviratne (1963) has discussed the functional significance of the disparity of the areas in the cat's L.G.N., citing the presence of the tapetum in the upper retina, as being the post retinal mirror (Granit, 1943; Weale, 1953; and Campbell, 1961). He pointed out that such intraocular scattering of light by the tapetum would tend to diminish the acuity of the retina; hence the representation of the lower field on the larger area of the L.G.N. may represent a compensatory adaptation, giving the cat enhanced sensitivity and acuity in the lower visual field.

2. The magnification factor

The magnification factor, defined by Daniel and Whitteridge (1961) as mm of receptive surface/degree of visual field, has been calculated in the horizontal meridian. When plotted together with the retinal ganglion cell concentration (Stone, 1965) against the retinal eccentricity, the magnification factor follows closely with the retinal ganglion cell density. There is also a close correlation between the region of greatest density of ganglion cells, and both vary in the same way with the retinal eccentricity in the frog (Jacobson, 1962). In the pigeon, the area of tectum devoted to any area of the retina is also proportional to the ganglion cell density of that area of the retina. There is a region of increased ganglion cell density immediately above a well developed fovea; there is also a corresponding large area on the lower surface of the optic tectum for the representation of this area (Whitteridge, 1965).

Comparison of the magnification factors in the S.C., and L.G.N. (Seneviratne, 1963) was made, and in general the same pattern was obtained. The differences may be regarded as insignificant, if the technical error and biological variation are taken into account.

The curve of retinal ganglion cell density as plotted is the result of the whole ganglion cell counts of the cat's retina without regard to their size (Stone, 1965). As a matter of fact, the optic fibers conveying impulses to the S.C. are only a fraction of the whole optic nerve fibers which travel mainly to the L.G.N. and include a small number to the pretectum and the accessory optic tract system. There is some agreement between electrophysiological and anatomical data that different sizes of optic fibers terminate in different visual centers. Bishop and Clare (1955) have reported, using electrophysiological methods, that the fibers of the optic nerve show 4 groups which differ in conduction velocities. Although there is some argument about the fiber grouping, the evidence from anatomical as well as electrophysiological data is in agreement that the larger fibers terminate in the L.G.N., and the small fibers end in the S.C. (Barris, Ingram and Ranson, 1935; O'Leary, 1940; Altman, 1962; Singleton and Peele, 1966; Bishop and Clare, 1955; and Altman and Malis, 1962).

Stone (1965), besides the total ganglion cell counts, has also measured ganglion cell diameters, and found that, in general, the cells are smallest in the central area and increase in size as density decreases. The distribution in the retina of different cell sizes groups is also shown. Among the 5 groups, two of them with diameter 8-10 u and 11-15 u, represent a large number of the total population. The distribution curves of ganglion cells of these two groups show a maximum at the central area and fall off rapidly towards the periphery of the retina. These two distribution curves have shapes similar to the curves of the magnification factors in the S.C. and L.G.N. If the fiber size is actually related to the size of the ganglion cells (Maturana, 1959), the ganglion cell groups may be correlated to the terminal structures, in these cases the L.G.N. and S.C. The picture becomes more complicated if some small fibers to the S.C. are branches from the larger fibers going to the L.G.N. as suggested by O'Leary (1940). This is supported by Granit (1955) who stimulated the colliculus and pretectum, and picked up impulses from the single, large retinal ganglion cells, and has also been confirmed by Chang (1956). Furthermore, since the midget ganglion cells of animals with fovea are small, and the ganglion cells in the area centralis retinae of animals that only possess a central region with greater cone density likewise belong to the smaller category, it is clear that specific messages from cones, in so far as they exist, will be conducted in the relatively small fibers (Granit, 1962).

B. SINGLE UNIT ACTIVITY IN THE SUPERIOR COLLICULUS

Only a few reports of single unit studies of the cat's S.C. have been described, in contrast with the detailed studies in the geniculostriate system.

Altman and Malis (1962), using diffused light as a stimulus, studied the behaviour of units. They found that the depth at which optically driven unit discharge disappears varied in different animals (mean depth 1.2 mm). This depth corresponds to the lower part of stratum opticum. According to the present results, the lowest limit of the photically driven units is the lower limit of the stratum griseum intermediale, not the stratum griseum superficiale as suggested by Altman and Malis. It is likely that their failure to drive the units is because the majority of the units in the lower part of stratum opticum and most of the units in the stratum griseum intermediale require more complex stimuli than in the superficial layer in which the non-directional unit can be stimulated by their diffuse illumination. In addition, they have described the spontaneously discharging units at depths varying from 0.8-3.0 mm from the surface of the S.C. which were non-visual. This corresponds to the layer at which unit responses can be elicited only by a specific stimulus.

More recently, Marchiava and Pepeu (1966) have reported preliminarily the single unit activity in the cat's S.C. Most of their units responded to moving stimuli, only a few of them responded to the absence or presence of light. They classified units responding to moving stimuli into 2 groups. One group, 23 units, required a movement about 6°-12° across, and the other group, 18 units, required a larger extent of movement, about 30-45° across. They have not mentioned either the site of recordings in the layers of the S.C. or the velocity of the stimuli used.

1. Small receptive field unit

The small receptive field units were obtained exclusively from the upper part of the stratum griseum superficiale. It must be mentioned that the structure responsible for the units in the upper part of the S.C. is a fiber layer (stratum zonale) as well as the stratum griseum superficiale. The stratum zonale in the cat, as described by Huber and Crosby (1943), consists of only a narrow band of fibers with small intercalated neurons, and the thickness of this layer as seen in the histological sections in this series of experiments is very thin, not more than 0.1 mm. These units were obtained from a wide extent (down to 0.4 mm from the surface). Because the action potential of the unit is of lower amplitude and is usually lost in the background noise or just above it, its shape cannot be identified as cell or fibers. If the units were recorded from the fiber layer, they should have a cortical origin as suggested by anatomists. Cajal (1955), Altman (1962), and Singleton and Peele (1966) failed to observe primary optic fibers reaching the uppermost layer, the stratum zonale. The positive evidence was obtained by Altman (1962) who has found, after a cortical lesion, a very small but distinct band of fibers terminating in the stratum zonale of the cat. He gives further evidence that these fibers may be followed directly from the brachium as a thin band of horizontal fibers moving over the dorsal surface of the S.C. The cortical origin of stratum zonale has also been reported in the rat (Lund, 1966) as a few degenerating fibers running in the stratum zonale.

The units with the characteristics of "small receptive field unit" have not been described in the cat's visual cortex. In addition, the present experiment on cooling the corresponding part of the visual cortex (visual I) failed to abolish a small receptive field unit. Thus it is unlikely that these units were recorded from the stratum zonale.

The possibility of retinal origin of a small receptive field unit may be considered. Examining the available data recorded from the retinal ganglion cell or the optic nerve, the preliminary report by Stone and Fabian (1966) shows only the existence of "on-off" units. They have described the receptive fields of 50 units recorded from the area centralis, in which 16 of them with "specialised fields" were classified into 3 groups. One group (4 units) showed "on-off" response with no maintained activity, the diameter ranging from 1/2-1 1/2°. Only one unit in their category showed a directional selectivity. So far, they have described this kind of unit in the area centralis. Whether specialised units exist in the peripheral retina or not has to be investigated. The failure to find the directionally selective units by previous authors (Wiesel, 1960; Rodieck and Stone, 1965) may be due to a very small percentage of the units which are scattered in the relatively small number of ganglion cells, and the possibility of selective recording by the electrode.

However, Humphrey (1967), in his brief note, has reported units in the superficial cell layer of the rat's S.C., as having a circular field of 5-10° across. Most of his units responded to moving stimuli and gave "on" and "off" response over the whole field.

On the other hand, Hughes (1966) recorded from the rabbit S.C., and described "small field off" units in the upper 0.2 mm from the surface. These units gave only an "off" response with marked lateral inhibition, and maintained discharge was not very common. He also described "on-off" units of 0.5 to more than 10° in diameter, in which some of the characteristics can be compared with small and medium-sized receptive fields in the present series. In addition, he has noted that the unit was very sensitive to movement.

2. Medium and large receptive field units

In the retina, Stone and Fabian (1966), have described a diffuse receptive field which is one type of their 'specialized field' group. This type of units has a larger receptive field, small center and large surround, with oscillatory responses to flashing stimuli. The responses to movement have not been investigated.

The more comparable type of receptive field with the "large receptive field unit" in the present series has been described by Barlow, Hill and Levick (1964) in the rabbit retina. They have described "large field type units" and have noted that units were very sensitive to movement. Both bright and dark spots gave very vigorous responses if the movement was fast enough. They also showed the responses of a large field unit to a rapid movement, and the fastest velocity in their records, is up to 290°/sec., in which a good response can still be elicited.

In the tectum of the frog, Lettvin, Maturana, Pitts and McCulloch (1961) have described the large receptive field units in which they termed "newness neurons". These cell bodies lie in the outer zone of a granular layer beneath the palisade layer, and have receptive fields about 30° in diameter. Such a neuron responds a little to sharp changes in illumination. They have remarked that marked adaptation is also an important characteristic of their units.

The size of the receptive field

One of the interesting findings in the present results is the size of a receptive field of "small receptive field unit" which is recorded from the upper part of the stratum griseum superficiale. The results show that the receptive field in the periphery still has a field size as small as the central field,or near central (2°-3° in diameter). Seneviratne (1963) measured the size of the receptive field units in the cat's L.G.N. and has described the small receptive field (1-2° in diameter) within 10° from the center of fixation and 4-6° in diameter or more beyond 25° from the center. Generally speaking, the size of receptive fields increases from the central to the peripheral. Hubel and Wiesel (1962) have also suggested that in more peripheral parts of the retina the field of cells in the cat's visual cortex tended to be larger than in the central part.

The differences in the distribution of receptive fields in the geniculostriate and the collicular system may reflect the functional differences of these two systems. The former concerned with visual perception would require a high degree of resolution for good visual acuity in the central region than in the peripheral part; whereas the latter, being concerned with functions other than visual perception, e.g., eye movement control, would depend on pericentral or peripheral fields as much as on central fields.

Another aspect of the receptive field size is that, in general, the deeper the recording sites the larger the receptive field. This generalization has also been noted by previous authors. In the rabbit's S.C., Seneviratne (1963) observed the small receptive fields in the collicular surface, and the fields becoming progressively larger in size with increasing depth of electrode. This view has been confirmed by Hughes (1966), extending the work by studying the units in the rabbit's S.C. in detail. In the rat's S.C. (Humphrey (1966) has also found receptive fields in the stratum griseum superficiale, 5-10° across, and 30-90° in the lower layer corresponding to the stratum opticum.

3. Directionally selective unit

Directionally selective units have been described in the retina of the rabbit (Barlow, Hill, and Levick; 1964), frog (Maturana, 1960), and pigeon (Maturana and Frenk, 1963); the tectum of the frog (Lettvin, Maturana, Pitts and McCulloch, 1961) and rabbit (Schaeffer, 1962); the lateral geniculate nucleus of the rabbit (Arden, 1963) and cat (Kosak, Rodieck and Bishop, 1965)and the striate cortex of the cat and monkey (Hubel, 1959; and Hubel and Wiesel, 1959, 1962); and very recently in the retina of the cat (Stone and Fabian, 1966; and Spinelli and Weingarton, 1966); and the optic nerve of the monkey (Michael, 1966).

Hubel and Wiesel (1959, 1962), in their description of "complex receptive fields", which were recorded from the cat's visual cortex, have described the directionally selective units. The most effective rates of movements for their units varied from cell to cell, from about 0.1° to 20.0°/sec. On rare occasions, inhibition of resting discharge in the null direction has been observed.

From available data, it seems that the directionally selective units exist in the retina of lower animals and in the higher visual centers of higher animals, e.g., cat and monkey. Brown and Rojas (1965) have also studied the receptive fields of retinal ganglion cells in the rat, and they found no directionally selective units, nor did Rodieck and Stone (1965, a, b). In the cat's retina, however, Stone and Fabian (1966) in their preliminary report, have shown a directionally selective unit to exist in the cat's retina, by recording from the area centralis. This is supported by Spinelli and Weingarten (1966) who also found a directionally selective unit in the cat's retina.

The existence of specialized units, e.g., directionally selective units in the cat's retina, may be regarded as an important observation. Hubel and Wiesel have suggested that more complex receptive fields recorded from higher visual centers resulted from the activity of units with concentric fields in the lower visual pathway and recombined in some simple fashion. This hypothesis may need revision.

Attempts were made to explain the mechanism of a directionally selective unit. It was thought by Hubel and Wiesel (1962) that the mechanism of a directionally selective unit in the cat's visual cortex could be explained by asymmetrical arrangement of the 'on' and 'off' zones in the receptive fields, and the interaction of effects summated over these zones. On the other hand, Barlow and Levick (1965), after the detailed description of the directionally selective unit in the rabbit's retina (Barlow, Hill and Levick, 1964), have investigated the mechanism of their directionally selective units. This led them to the conclusion that "the ganglion cells responding to a particular direction are fed by subset of bipolar cells that respond to the corresponding séquence of excitation of two neighbouring retinal regions with which they connect". Furthermore, they have advanced their evidence that this sequence discrimination is brought about by laterally connected inhibitory elements from one of these regions, and this seems to be a likely function for the horizontal cells to perform.

The special type of directionally selective unit described in the present study, which has been called "centrifugal unit" has not been reported in the visual system. However, by the term "response to centrifugal movement" reported by Andrew (1955, quoted by Lettvin, Maturana, Pitts and McCulloch, 1961) is meant a stimulus moving away from the center of the receptive field in the frog's tectum, which is different from the "centrifugal unit" in the present study. The physiological significance of the centrifugal unit will be discussed together with the centrifugal unit in the cerebellar visual area in the last section.

4. Specific orientation unit

In the cat's visual cortex Hubel and Wiesel (1959, 1962) were the first to describe the receptive field which requires placing or moving of a stimulus in a particular orientation, and the orientation of the receptive field axis varies from cell to cell.

In the present experiments, receptive fields with such behaviour have been recorded from the stratum opticum. In the present series, most of the units gave sluggish responses to a stationary spot of light or stationary light bar; good responses can only be elicited by moving stimuli in contrast to the cat's visual cortex, described by Hubel and Wiesel (1959, 1962, and 1965), in which the majority of units responded to stationary stimuli. However, they also described the moving stimuli in studying cells that gave little or no response to stationary patterns.

In view of the behaviour of specific orientation units in the present study which are very similar to units in the cat's visual cortex (Hubel and Wiesel, 1959, 1962), the question arises whether these responses have been recorded from the axons of cortical cells or have originated in the collicular cells themselves. The problem can be answered, since on one occasion at least, a unit still fired spontaneously in spite of the loss of the visual responses when a corresponding part of the visual cortex had been cooled.

In other species, units selected for the orientation of targets have also been found in the pigeon retina (Maturana and Frenk, 1963) as well as in the rabbit retina (Levick, 1967). In both species, the specific orientation units with receptive field on the horizontal and vertical preferred orientations have been observed. Levick (1967) also discussed the usefulness of this unit system in the rabbit by citing the experiment of Vanhof (1966) who has found that the rabbit can discriminate between the striped pattern of different orientations, other than horizontal and vertical. This has led Levick to write "there seems little doubt that the rabbit uses information other than that provided by the retinal orientation-selective system in the 45°-135° discrimination task".

C. INFLUENCE OF THE VISUAL CORTEX UPON THE SUPERIOR COLLICULUS

The present study establishes that some cells in the S.C., especially in the stratum opticum, have received facilitatory influences or control from the corresponding regions of the visual cortex, (visual I), in response to visual stimuli. The possibility that the visual cortex may exert a facilitatory influence on visual responses at the S.C. via a cortico-collicular pathway was suggested by the finding that ablation of the visual cortex reduces the amplitude and lengthens the latency of collicular responses to visual stimulation (Ingvar and Hunter, 1955; and Clark, 1942). Recently Jassik-Gerschenfeld, and Ascher (1963) have reported that visual collicular responses were increased by strychninization of the visual cortex and decreased (but not abolished) by depression or ablation of the same area.

Most of the units, abolished by cooling in the present study, were in the stratum opticum, only 2 of them were in the upper part of the stratum griseum intermediale. These findings, in general, seem to be consistent with the termination of fiber degenerations from cortical lesions.

In the cat, Altman (1962) reported that, the cortical fibers are distributed separately through the stratum zonale, stratum opticum, and stratum griseum intermediale. Some fibers form a dark band in the stratum opticum and penetrate dorsally into the stratum griseum superficiale, and ventrally into the stratum griseum intermediale. The largest bundle of corticofugal fibers is concentrated in the stratum griseum intermediale and the majority of them come directly from the brachium rather than via the stratum opticum. Another worker, Sprague (1963) has also reported the terminal degeneration, chiefly in the stratum opticum and stratum griseum superficiale, less in the superficial part of stratum griseum intermediale after lesions placed in the caudal pole of the lateral gyrus or in the middle part of the postero-lateral gyrus. These results, however, are in agreement with a recent report by Lund (1966) in the rat, who has found that the fibers of cortical origin running in the stratum opticum terminate in this layer and principally in the deeper part of the stratum griseum superficiale.

The two types of units which were found to be abolished by cooling the visual cortex are the specific orientation units and non-directional units. The units which have specific orientation properties have been reported in the cat's visual cortex (Hubel and Wiesel, 1959, 1962). The abolished units may be recorded from the axons of these cortical units. This possibility can be ruled out by the observation that in spite of the disappearance of the visual response but one unit, at least, in this category still showed spontaneous activity.

This also happened in the non-directional units, in which spontaneous activity still remained in one unit. Moreover, some of them showed the characteristics of cell spikes. We do not know whether these cells receive the visual input exclusively from the visual cortex or dual inputs from both the visual cortex and direct retinotectal pathway. If the collicular cells mentioned above receive dual visual inputs, the visual response should be reduced or altered instead of completely disappearing after the blockage of one input. Whatever the true function of the S.C., Lund (1966) suggested that its response to visual stimuli, at least in some cells, may be the result of the interaction of two inputs from the visual cortex and retina rather than the autonomous functioning of one in the absence of the other, as is often assumed in behavioural experiments. The possibility of contralateral cortical influence on collicular responses should be considered. The work of Jassik-Gerschenfeld, Ascher and Guevara (1966) has demonstrated that although the main effect of the visual cortex is exerted on the ipsilateral colliculus; there also exists a contralateral facilitatory influence, apparently mediated predominantly by intercollicular commissure. However, in the present experiments, the corresponding region of the cortex on the contralateral side as well as the ipsilateral cortex was cooled, because the cooler was placed in the interhemispheric region.

In responses to photic stimulation, the latency of the cortical potential is 7 ± 1 msec. shorter than the latency of the corresponding collicular response (Altman and Malis, 1962; Harman and Berry, 1956). The cortico-collicular conduction time, measured by spontaneous strychnine spikes and electrical stimulation of the visual cortex, is about 2-2.5 msec. (Jassik- Gerschenfeld, Ascher and Guevara, 1966). If the time difference between the conduction of impulses along the retino-geniculo-collicular pathway and direct collicular pathway is allowed for "intracortical relay", both visual impulses should reach the S.C., more or less, at the same time, or with very little difference.

Another view of the interaction of the visual cortex and S.C. in the cat has been reported preliminarily by Sprague (1966) in his behavioural study. The evidence of interaction as a mediation of visually guided behaviour is as follows; the initial hemi-anopia from ablation of the visual cortex is apparently due to the depression of the function of the colliculus ipsilateral to the cortical lesion, maintained by inhibition of the opposite colliculus,because subsequent removal of the contralateral tectum or splitting of the collicular commissure abolishes this inhibition and allows the return of function in the ipsilateral colliculus with recovery from hemi-anopia. Sprague emphasizes that "visually guided behaviour" is mediated at both cortical and midbrain levels, and that there is a marked interaction between these sites.

The influence of the visual cortex on the colliculus in the present experiments was studied under chloralose anaesthesia, the same anaesthetic used by Jassik et al (1963, 1966). On the other hand, Altman and Malis (1962) could not demonstrate this interaction. In view of the observations in the unanaesthetized animal, the collicular responses to electrical stimulation of the visual cortex are easily observed (Ingvar and Hunter, 1955), and that in the same preparation ablation of the visual cortex reduces collicular response to photic stimulation. These results suggest that a cortical control of the S.C. exists under normal conditions. The negative findings of Altman and Malis (1962) were probably due to a deep nembutal anaesthesia.

D. FUNCTIONS OF THE SUPERIOR COLLICULUS

"The role of the superior colliculus in vision must of necessity be greatly dependent upon the extent to which a geniculo-striate system has developed ...... In mammals higher than rodents, control of eye movements is likely to be the most important function of collicular optic projections and possibly activation of non-specific visual afferents." (Granit, 1962).

"In lower animals, such as the cat, we may conclude that the colliculi are centers for visually directed movements". (Davson, 1963).

The functions of the cat's superior colliculus can be considered as two problems, as the role in vision and the role in eye movements. In fact, the problem of whether the former and the latter functions are related or not, or are dependent upon each other, has to be borne in mind.

1. Role in vision

Since both brightness and flicker discrimination are visual functions which can be relearned after complex ablation of the visual cortex (Smith, 1937; Baden, Urbaitis, and Meikle, 1965), it is obvious that visual pathways other than the geniculo-striate projection system can convey the information needed for these discriminations. The superior colliculus would seem to be the possible relay point for such information. This is supported by the deficits in visual discrimination after secondary lesions of the cat's tectum following removal of the visual cortex (Norton and Clark, 1963; and Fischman and Meikle, 1965).

Sprague and Meikle (1965) have described an homonymous field defect with complete neglect of stimuli in the visual fields contralateral to the lesions in the S.C. of the cat which do not involve tegmentum. Associated with these are abnormal responses to contralateral acoustic, tactile and sometimes nociceptive stimuli, appearing as inappropriate localization of the stimuli rather than as changes in sensory threshold. In addition, lesions placed in certain afferent and efferent collicular pathways, involving the brachium of the S.C., the sub-collicular tegmentum, result either in no visual neglect or in deficits which are minimal or transient. Their findings have led them to conclude that "the functions of the S.C. include that of visual attention and perception as well as the clinically accepted control of the movements of head and eyes".

On the contrary, lesions which have destroyed the S.C. bilaterally caused only very transitory disturbances of performance on the series of difficult visual pattern discrimination tasks. On the other hand, prolonged disturbance resulted from quite similar lesions which have had, in addition, extension of the destruction to either central gray substance or the ventrally adjoining tegmentum. Furthermore, effects of similar magnitude have been obtained after lesions restricted to the tegmentum of the midbrain. (Myers, 1964).

However, Sprague (1966) in his recent preliminary report, has extended the work into the interaction of the visual cortex and the S.C. in mediation of visually guided behaviour. His evidence is as follows: the vision returns, from total contralateral hemianopia following unilateral removal of the occipito-temporal neocortex in the cat, after the contralateral S.C. has subsequently been removed. Splitting of the collicular commissure produces the same result as the removal of the contralateral tectum. Sprague has put forward the hypothesis that the colliculus is functionally depressed because there is an inhibition resulting from an imbalance of visual centers after a cortical lesion and the recovery is the result of the removal of an inhibition from the S.C. on the opposite side.

2. Role in eye movements

(a) Afferent mechanisms

The role played by the S.C. in afferent mechanisms may be considered in two ways, the information from the retina on one hand, and from the extraocular proprioceptors on the other hand.

Information from the retina

The present experiments have dealt with this problem. Apart from the confirmation of the precise retinotopic organization in the superior colliculus, it has been shown that there are units in the S.C. of the cat which respond to movement of different velocities, some showing directional selectivity, and centrifugal preferences in some units. The small receptive field unit with simple behaviour is found in the superficial cell layer and the receptive field is increased in size and complexity of behaviour in the deep layers.

The superior colliculus has been shown to participate in the fixation by some authors, e.g., Dreher, Marchiafava, and Zernicki (1965). Let us imagine that the cat's eyes are stimulated by an object somewhere in the peripheral field. Attention is aroused and the eyes move so that the image of the object approaches the area centralis. To change fixation to the new target, the cat needs to know the position of the new object; to accomplish this, he has the precise retinotopic organization on the surface of the S.C., to cope with this task. The course of movement in changing the fixation has a velocity of about 100-200°/sec. (Dreher, Marchiafava, and Zernicki, 1965) in the cat. In humans the speed of shifting the fixation from one point to another appears to be more or less constant and independent of voluntary control. Hyde (1959) reported a mean velocity of

485°/sec. for a movement of 60°. Westheimer (1954) found the maximal velocity to increase as a function of the amplitude of the movement. To reach the new target with accuracy, a directionally selective unit may serve this purpose, for checking the direction, and a centrifugal preference unit responding to fast movement may provide information to prevent overshooting of the saccadic movement,which is so rapid.

Apart from finding stationary objects, dealing with moving objects so as to keep them in the area centralis is a more difficult task; again, the centrifugal unit responding to different velocities may serve this purpose. (The role of a centrifugal unit will be considered, together with a centrifugal unit in the cerebellar visual area, in a later section).

Proprioceptor as an afferent mechanism

The role of a proprioceptive mechanism has been reviewed by Cooper, Daniel and Whitteridge (1955), and Whitteridge (1960. 1962).

In the cat, although extraocular muscles lack muscle spindle, they possess many sensory endings, some of which can be activated by passive stretch. Discharges from these proprioceptors were recorded in the fibers of the third nerve in the orbit (Cooper and Fillenz, 1952, 1955). Apart from the early sustained responses along the course of the mesencephalic tract of N V from the pulling of the eye muscles of the cat, Fillenz (1955) has found late responses in the deep layer of the S.C. (stratum opticum). This finding has led this author to suggest that the information from the retina and from the proprioceptors of eye muscles are associated in some of the lower visual reflexes. The impulses from muscle spindles recorded in the stratum opticum of the goat's superior colliculus has also been previously reported by Cooper, Daniel, and Whitteridge (1953). These authors have also discussed the functional significance of the impulses from the eye muscle proprioceptors. They have cited evidence associated with the relative speeds which reach the brain. The responses set up by illumination of the retina reach the brain much later than those from the sensory endings in the muscles; largely owing to the retina delay. The messages from the proprioceptors reach the brainstem with latencies dependent only on their conduction time, i.e., in 1 or 2 msec. They have suggested furthermore that "by the time the retinal discharges reach the brain, messages from the eye muscles can have been sent to all the centers that may be concerned with the integration of ocular movements. The eye muscle neuronal pools will then be in a state of readiness to control the delicate muscular movements needed for maintaining fixation".

(b) Stimulation experiments

That stimulation of the superior colliculus produces conjugate deviation of the eye has been confirmed in the cat (Hess, 1956; Hyde and Eliasson, 1959). Moreover, eye movements may be elicited by illumination of the retina following local application of strychnine to certain areas in the collicular surface (Apter, 1946). Based on their findings of stimulation experiments in cats with an implanted electrode, Hess, Burgi and Bucher (1946) elaborated a theory of what they called "visual grasp reflex" according to which the colliculi would be the centers for the fixating mechanism of objects in motion. Hyde and Eliasson (1957, 1959), have called the final position of the eye after stimulation of the cat's S.C. "goal directed". The position of the "goal" varied with the region of the S.C. stimulated, and more or less coincided with the electrophysiological map of the visual field on the S.C.. Their average maximal velocity in any single eye movement upon stimulation ranged between 40-150°/ /sec. for different sites. In occasional individual responses a maximal speed of 300°/sec. was recorded.

Hyde (1964), in her study on the interrelationship of brainstem and cortical areas for conjugate ocular movements in the cat, has suggested the collicular-oculomotor pathways, as studied by lesions in the encéphale isolé cat.

Impulses from the S.C. appear to descend through the lateral pontine tegmentum after decussation, traversing the medial reticular substance of the medulla. Finally, they enter the medial longitudinal fasciculus to ascend to the third nucleus.

Several routes have been postulated for the efferent occipital cortical pathways to the eye muscle nuclei. These include corticotectal connections and fibers passing the S.C. (Crosby, 1951; and Hyde, 1960). However, Hyde (1964) also suggested that the efferent paths from the occipital cortex and superior colliculus are separated at least in the midbrain level. The lesions in the medulla were without effect on oculomotor responses to occipital cortical stimulation although abolishing collicular responses. This has led this author to conclude that no single anatomically circumscribed center can be found that appears to co-ordinate all types of lateral gaze (Hyde, 1964).

(c) Ablation experiments

Early studies on the effects of lesions in the S.C. of the cat disclosed no impairment of eye movements following almost complete destruction of these areas (Spiegel and Scala, 1937). Moreover, conjugate eye movements in all planes could be elicited by stimulation of the frontal and occipital lobes in cats with extensive destruction of the S.C.

Blake (1959) reported that after collicular lesions there was no vertical eye following of objects, and that eyes moved to the opposite direction to that of moving targets in the horizontal plane. However, analysis of this report disclosed that the lesions extended beyond the colliculi into the pretectum and the mesencephalic tegmentum. Optokinetic nystagmus was found to be impaired after lesions in the S.C. of the cat (Scala and Spiegel, 1938).

The anatomical evidence of direct connections between the S.C. and the oculomotor nuclei has been denied by some investigators (Marburg and Warner, 1947; and Altman and Carpenter, 1961) but strongly postulated by Bucher and Bergi (1950). However, the interstitial nucleus of Cajal has been described as a relay for the colliculo-oculomotor pathway. Its large nerve cells give rise to the particularly large interstitiospinal fibers which constitute the medial border of the medial longitudinal fasciculus and they send collaterals to all eye muscle nuclei (Jung and Hassler, 1960).

Recent behavioural experiments by Myers (1964) and Sprague and Meikle (1965) revealed some motor disturbances following restricted removal of the S.C.. The former author described a marked reduction of movements of visual regard. In addition, visual centering and following movements are difficult to elicit and when obtained are greatly inaccurate.

The latter authors have reported a motor deficit in appropriate movements of eyes, head and body, expressed in ipsiversive forced circling and heightened compulsive response to ipsilateral stimuli. Bilateral lesions result in the following defects:- first post-operative week, the cats showed an inability to look upwards spontaneously and failed to localize small stationary objects, or to follow a more rapidly moving stimulus. In subsequent weeks, no change was observed until the tenth week when eye movements to lateral rotation were good, but were minimal to vertical tilting.

The effects of tectal lesions and cortical lesions on the fixation reflex of the eye-ball were investigated in the cat by Dreher, Marchiafava, and Zernicki (1965) before and after midpontine pretrigeminal transection. The vertical fixation reflex to all visual stimuli, both stationary and moving in front of the animal's eyes, seemed to have completely disappeared after removal of superior colliculi; while there was very strong impairment of the horizontal one. The ablation of the frontal oculomotor area did not effect the fixation reflex. After ablation of the occipital cortex, the fixation reflexes, both vertical and horizontal, were impaired. Furthermore, vertical eye movements in the cat without either occipital cortex or tectum can be elicited by stimulation of the frontal oculomotor areas. Stimulation of the visual cortex produced eye movements in cats without frontal cortex.

These effects could not be elicited in cats with the tectum removed. They have postulated that the fixation reflex arc is subdivided into 2 branches, occipital and tectal. Both seem to be partially independent in the horizontal fixation reflex.

III. THE SUPERIOR COLLICULUS OF THE BABOON

A. RETINOTOPIC PROJECTION ONTO THE SUPERIOR COLLICULUS

The present experiment has established that apart from the retinotopic organization on the surface of the S.C., there is a representation of the fovea onto the anterior pole of the S.C.. The problem of the macular representation on to the S.C. has started since the study of termination of optic centers of the monkey by Brouwer and Zeeman (1926) after retinal lesions. These authors could not find degeneration after macular lesions. This has led Whitteridge (1960) to suggest that macular fibers may relay in the L.G.N. A study of photically and electrically elicited responses in the central visual system of the squirrel by Doty, Kimura and Mogenson (1964) has revealed that the latency to the S.C. by strong light flash was about 22 msec. which was 3-6 msec. longer than that to the L.G.N..

Another possibility is that the macular fibers may be relayed from the visual cortex because cortico-collicular fibers have been shown to exist by several investigators. Crosby and Henderson (1948) have traced occipito-collicular fibers from area 18 and 19 in the macaque. These cross the pulvinar and run back adjacent to the posterior commissure to enter the S.C. in the deep part of the stratum opticum.

Other anatomists have traced fibers to the colliculi only from area 17, either from the convexity (Beevor and Hossley, 1902; Clark, 1941, 1942) or exclusively from the medial aspect of the occipital lobe (superior lip of calcarine fissure) (Mettler, 1935). It is unlikely that the macular fibers terminating in the S.C. have originated from the visual cortex, not directly from the retina, because the latencies from the retina to the S.C. and striate cortex by light stimulation under relatively the same parameters have been observed, and the values of about 30-40 msec. were obtained respectively. In addition, the early visual responses by photic stimulation with a latency of 30-60 msec. have been observed in the striate cortex of the baboon (Daniel and Whitteridge, 1961).

The surface areas of the S.C. found in the present experiments to be devoted to the representation of the lower and upper visual fields are equal. The same observation was obtained in the baboon's visual cortex in which the magnification factors along different radii were plotted against the retinal eccentricity and close correlation was obtained. (Daniel and Whitteridge, 1961).

In the baboon's retinal ganglion cells, although the horizontal meridian has some ganglion cell density, it has been found that the ganglion cell density falls off progressively with increasing distance from the fovea along any

any meridian (Whitteridge, 1965).

B. SINGLE UNIT OBSERVATIONS

Owing to the limitation of the numbers of experimental animals studied combined with the difficulties in the isolation of the unit, only a few have, so far, been observed. It is therefore hardly possible to make generalizations concerning the behaviour of units in the superior colliculus. In this aspect, comparison with animals of other species might be useful.

In the present experiments, the visual responses were obtained from the surface down to the lower part of the stratum griseum intermediale. The same result was obtained in the cat's superior colliculus described above. Two non-directional units in the present series had the receptive field size 3°-5° in diameter, and responded to relatively slow movement and were recorded from the stratum griseum superficiale. They were similar in behaviour to the small and medium-sized receptive fields of the cat's superior colliculus. In addition, two specific orientation units recorded in the stratum griseum superficiale and stratum opticum of the baboon's S.C. have also been described in the cat's superior colliculus in the previous section. Furthermore, though no detailed report of this kind of unit in the primate level exists, Hubel and Wiesel (1962) mentioned that the kinds of units described in the cat's visual cortex have also been found in the monkey's visual cortex. If the technical difficulties could be overcome, it would be interesting to study the influence of the visual cortex upon the unit activity in the S.C., as has been described above in the cat.

C. FUNCTIONS OF PRIMATE SUPERIOR COLLICULUS

The literature dealing with the function of the primate S.C. has been one of the controversial problems in the visual system.

The structure regarded as the most important subcortical visual and oculomotor integrating centers is the superior colliculus. But according to the theory of "progressive encephalization of function" as applied to vision (Marquis, 1935), the visual cortex takes over more and more of the functions of the tectum as one ascends the phylogenetic scale. The superior colliculi of higher mammals receive decreasing numbers of direct optic fibers and finally in the primate a few of these fibers can be traced to the superior colliculus (Brouwer and Zeeman, 1926).

With regard to oculomotor function, it has been suggested that the superior colliculi were the structure through which the occipital eye center operated (Holmes, 1938). This concept was further elaborated by Crosby and Henderson (1948) on the basis of their physiological and anatomical findings. These authors obtained a unique pattern of eye movements upon stimulation of area 19. Moreover, they traced several discrete bundles of cortico-tectal fibers in normal anatomical material projecting from area 18, 19 and possibly 17, to the superior colliculi, and from here a tecto-oculomotor tract to the oculo-motor nuclei. These descriptions were further supported by the findings of spike potentials recorded from the superior colliculi following application of strychnine to area 19 (Peterson and Henneman, 1948). The role of the superior colliculus in eye movements has been discussed in the review of "Central control of eye movements". (Whitteridge 1960). He writes: "In the lower mammals the colliculus plays a large part in adversive movements; in monkeys and man it is at least a distribution center for descending pathways for eye movements".

Regarding the role of the S.C. in vision, Ferrier and Turner (1901) have reported retention of grossly normal oculomotor function and vision, while Rosvold, Mishkin and Szwarcbart (1958) described fixed gaze following extensive collicular damage. However, there is no detailed histology in any of these reports.

Denny-Brown (1962) has reported that after bilateral removal of the S.C. in the monkey the animal suffers a temporary loss of vision. He writes "... even more extraordinary than this loss of vision following ablation of the colliculi was the changes in general behaviour of these monkeys. Whether some vision for movement and placing remained or not the animals appeared to be totally unaware of events in their environments". He also concludes that the primate tectum is essential for reactions which may be called visual awareness and that in general the tectum has initiating or facilitating function. It is especially noteworthy that his lesion in the superior colliculus causes no change in the pathway to the visual cortex via the lateral geniculate nucleus, and as the author points out, the normal cortical evoked potential is preserved after the tectal ablation.

On the other hand, Pasik and Pasik (1964) studied the role of the primates' cerebral cortex and superior colliculus in oculomotor function by the method of ablation and stimulation. Apart from the observation in the cerebral cortex, their results indicate that there are no centers for vertical or other eye movements. The superior colliculi are not necessary stations for the eye movements initiated in the preoccipital area. Regarding optokinetic nystagmus, these authors conclude that there are no centers for it in the vertical or any other planes in the superior colliculi. This is in contrast to the views of Carmichael, Dix and Hallpike (1954) who regarded the superior colliculi as a subcortical center for optokinetic nystagmus in all planes and by Crosby (1957) in the vertical plane.

From the available data, there are still contrary views as to the function of the primate superior colliculus, whether this structure still has something to do, e.g., eye movement mechanisms, and role in vision, or no function at all. However, whatever the function may be, the results of the present experiments show that the precise retinotopic organization still exists in the primate superior colliculus. Moreover, the complex behaviour of single units has also been observed. This structure still, therefore, has some functional significance in the participation of complex nervous mechanisms, e.g., eye movements, in spite of the decrease in size of the structure according to the phylogenetic scale of progressive encephalization of function.

IV. THE CEREBELLAR VISUAL AREA OF THE CAT

A. SINGLE UNIT ACTIVITY IN THE CEREBELLAR VISUAL AREA

1. General considerations

(a) Hbbituation

As already mentioned in the results of the present series of experiments, most of the visual units in the cerebellar visual area showed the behaviour of habituation to repeated stimulation. The term "habituation" has been used by Humphrey (1933) to refer to the waning of a behavioural response as the result of repeated stimulation. This is in contrast to the expression of sensory adaptation, which was used by Adrian and Zotterman (1926) to describe the waning of the impulse activity in the continued presence of the stimulus.

The habituation of unit responses to repeated sensory stimulation have been reported to occur in various animals. Hamdi and Whitteridge (1954) recorded action potentials from the optic tectum of pigeons. It was found that the responses to a flash of light of units in the innnerlayers of this structure "rapidly fatigued on repetition"; habituation of the response to repeated stimulation has also been described in the optic tectum of the frog (Lettvin, Maturana, Pitts and McCulloch, 1961), and in the rabbit's lateral geniculate nucleus (Arden, 1963).

Horn and Hill (1966) have studied the habituation of units in the rabbit's superior colliculus in some detail. They found that when the stimulus was repeatedly presented the response to that stimulus waned after 30 to 40 presentations. A change of some parameter of the stimulus, or of its position on the receptive field, was usually sufficient to re-excite the unit. If the stimulus was withdrawn for 20 sec. or so and then represented, cells would respond again. In general, and within limits, the longer the stimulus was withdrawn the more vigorous was the response likely to be on subsequent presentation.

Habituation has not been reported among units in the visual system of cats and monkeys. In the auditory system, Hubel, Henson, Rupert, and Galambos (1959) have described the habituation of units in the cat's auditory cortex. These results have since been confirmed by Galambos (1960), and Evans and Whitfield (1964). The mechanism responsible for attenuating the response to repeated sensory stimulation is quite obscure.

(b) Units which respond to fast movement

The majority of units recorded in the cerebellar visual area , as in the deep layer of the superior colliculus of the cat, required fast movements in a certain range (up to 300°/ /sec.) as the optimum stimuli. The question of whether these units are of physiological significance or not has to be considered in some detail.

As a matter of fact, many investigators have mentioned units recorded in the visual system as responding to fast movements but only a few of them have been reported quantitatively. Units which respond to fast movement have not been reported in the cat's retina, but have been described in the rabbit. Barlow, Hill, and Levick (1964) have described large receptive field units in the rabbit's retina which respond to a movement of fast speed, and the fastest velocity in their records is up to 290°/sec., in which a good visual response could still be obtained. They have noted that slow movement could not excite their units at all.

Apart from mammals, Collett and Blest (1966) have reported the directionally selective units in insects which could be excited optimally by moving stimuli at about 100°/sec.

Units responding to fast movement which have been shown to exist in the S.C. and the cerebellar visual area of the cat, so far, have not been described in the lateral geniculate nucleus and the visual cortex. These two latter structures of the geniculo-striate system would require a high degree of resolution for visual perception and pattern vision, so it would be expected that only stationary or slowly moving objects provide the optimum stimuli.

Miller and Reeder (1965) in studying kinetic visual acuity, found that if a target is moving at less than 60°/sec., saccadic eye movement is minimal and head movement is not necessary. About 60°/sec. restriction of the head movement lowers kinetic visual acuity and when a certain speed is reached (about 100°/sec.) both saccadic eye movements and head movements are employed.

Thus units responding to fast movement found in the cerebellar visual area and superior colliculus, which have nothing to do with visual perception, would serve as a regulating device for the precision of eye movements which are so rapid. Hyde and Eason (1959) have reported the characteristics of the cat's ocular movements evoked by stimulation of the brainstem. Upon stimulation, the eyes began to move at a rapidly accelerating rate, reaching a maximal velocity 0.125-0.25 sec. after the onset of stimulation. The average maximal velocity in any single series ranged between $40-150^\circ$/ /sec. for different sites. In occasional individual responses a maximum speed of 300°/sec. was recorded.

2. Non-directionally selective unit

Large receptive field unit

The units with very large receptive fields and which responded to a small excursion of movement of a small target all over the field described in the present experiment, have also been reported by Lettvin, Maturana, Pitts, and McCulloch (1961) in the frog's tectum. Their units respond to a small target, 1-2° in diameter, travelling around almost everywhere in the visual field but have a "null" region that is different for different cells. Every time the stimulus moves, with even a short jerk, there is a burst of impulses that dies down when the stimulus has stopped. However, they do not state either the velocity used or the optimum velocity of the stimulus for the cells. It should be noted that there is usually no response to turning "on" or "off" of the illumination in their units.

Medium receptive field

The units which respond to movement and show the behaviour of habituation after repeated stimulation, have not been described in the cat's visual system. In the frog, Lettvin, Maturana, Pitts, and McCulloch (1961) recorded from cells in the optic tectum. These cells which the authors called "newness" had a receptive field about 30° in diameter, and responded to movement in one direction along any particular diameter of the receptive field, but when this movement was repeated along the same path less than 5-10 sec. later, no response was elicited. With a delay of 20 sec. a response could be elicited again, but less than that evoked by the first movement. Movements along the different diameters of the receptive field were usually observed to elicit a brisk response.

Hughes (1966) has also described units in the deep layer of the rabbit's superior colliculus, with a receptive field about 20°-30° across. The main feature is their adaptation or habituation to repeatedly presented stimuli. He also noted the difficulty to study these units because part of the field may disappear and then return, or the whole region may become refractory.

3. Centrifugal unit

Units which require fast movement in a centrifugal direction as an optimum stimulus have been described in the cerebellar visual area and the deep layers of the superior colliculus in the present series of experiments. Units with such behaviour, so far, have not been reported in the visual system.

The movements of the two eyes brought about by twelve extraocular muscles of the animals with frontal eye field are very well co-ordinated. This co-ordination is an extremely delicate and important task since a fusion of an image from an object falls upon both foveae on the corresponding points on the two retinae. It is certainly surprising that the efferent discharges of the oculo-motor nuclei of both sides are so rapidly regulated, in spite of the fast speed of movement performed by both eyes. The main purpose of eye movement is to bring an interesting object into the central portion and keep it there in order to use a high density of ganglion cells for a high degree of resolution of visual acuity.

An object may accidentally move away from the central retinal region by either a movement of that object itself or by a movement of the animal (If the animal moves forwards, the object in front but not in the center tends to move away from the central region of the retina.) The centrifugal unit may play an afferent role for regulation of these conditions; control of eye movements in the former case and control of the orientation of the animal's movement in the latter case might be a possibility.

Collett and Blest (1966) have also described some units in the optic lobe of the moth which responded to fast movement. These units showed a directional selectivity in which movement from front to back was the preferred direction. The authors pointed out that these units may function to control orientation when the moth has a little forward velocity. More detailed studies are needed before it is known whether these units provide adequate information to control orientation while a moth is flying fast. The units recorded in the superior colliculus and the cerebellar visual area may have a similar function to control the orientation of movement.

The impulses from the proprioceptors of the eye muscles have been mentioned to reach the cerebellum and the deep layers of the superior colliculus in the goat by Cooper, Daniel, and Whitteridge (1953). In addition, various patterns of eye movements in the cat have been described by various investigators, recently by Cohen, Goto, Shanzer, and Weiss (1965).

Cats, after the cerebellar audio-visual area had been removed, showed some disturbances in the auditory and visual systems. (Chamber and Sprague, 1955). In the postoperative period, the cats showed rather marked difficulties in gauging distances properly when jumping, reduced movement of the eyes and the head, and increase in post-rotatory nystagmus. By the sixth day the response to visual cues was back to preoperative alertness, although there was a marked tendency for visual attention to become fixed for considerable periods.

In humans, Cogan (1954) has reported ocular abnormality in 6 patients with cerebellar diseases in which he called "ocular dysmetria". This ocular abnormality is manifest most commonly by overshoot (rarely undershoot) of the eyes on change of fixation. Instead of the precise movement of the eyes which is the invariable response of the normal person, these patients show an overshoot with several oscillations of diminishing magnitude before the eyes come to rest. In one patient, after eccentric fixation the eyes overshot as much as 30° in returning to fixate on a point straight ahead. The exact cerebellar lesions have not been mentioned, however, and it is difficult to interpret the extent of the lesions resulting from disease which are usually extensive.

The units which respond to fast movement positioning around the central region of the visual field, and some showing centrifugal preferences in response to movement, may provide the information to prevent overshooting of the eye movements in changing the fixation, and also provide the information to the oculomotor system when the fixated object suddenly moves out from the center of fixation.

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