FACTORS WHICH DETERMINE VISUAL ACUITY

A Thesis

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by

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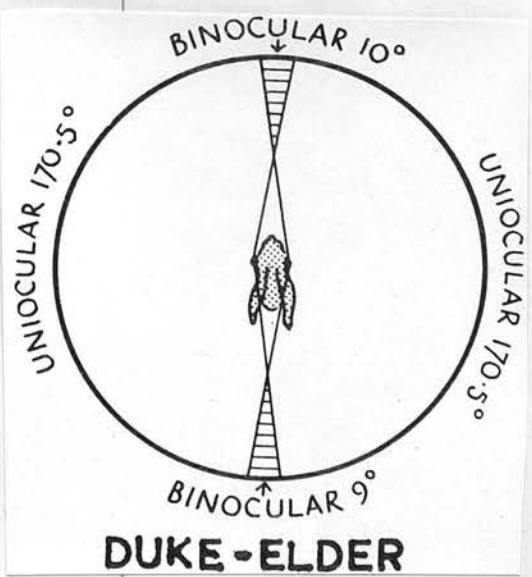
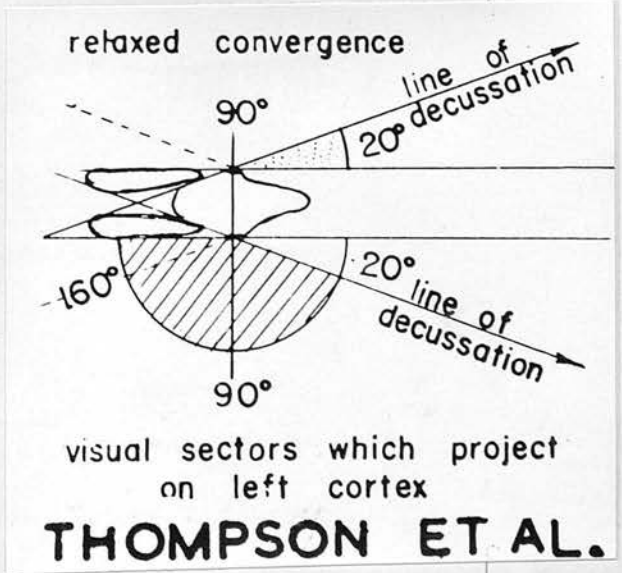
INTRODUCTION

A. ANATOMICAL OBSERVATION

I THE EYE

In the rabbit the orbits open laterally, the axis making an angle of 80 - 85 degrees with the sagittal plane of the head. They are shallow with incomplete bony floor, the deficiency being made up by muscles. The shallowness of the orbit makes the eye protrude considerably out of the socket. This gives the rabbit a wide range of monocular vision. (Davis 1929, Duke-Elder 1958 and Sheppard 1961). The panoramic field of the rabbit, in Duke-Elder's (1958) opinion, consists of a small binocular segment 10° in front and 9° behind and a large uniocular area, 170.5° on each side. This is in disagreement with Thompson, Woolsey and Talbot's (1950) view, who deny any binocular overlap behind and extend the anterior binocular field to 20°, when both the eyes converge, the monocular field being 160°.





The state of refraction in the rodents is rather confusing. In their natural surrounding the rabbits are supposed to have a very high degree of hypermetropia, as high as +7 or +10 D. The nocturnal species particularly are unperturbed by this as they obviously depend visually on the appreciation of differences of luminosity and movement rather than on the very imperfect pattern vision of which their eyes are capable. But under domestic surroundings they tend to develop high degree of myopia (Duke-Elder 1958). Thompson (1958) thinks that the rabbits are hypermetropic and it is to the tune of +5 D.

II THE RETINA

The rabbit's retina attracted the attention of the anatomists at a very early date. Polyak (1955) claims the priority of observation of the characteristic "fanlike arrangement" of the optic nerve fibres leaving the optic nerve head for Briggs in 1685. The subsequent observers are Morgagni in 1719, Valsalva in 1740 and Zin in 1754 (quoted by Polyak 1955) and Cuvier in 1845 (quoted by Davis 1929). The band of myelinated fibres streams nasally and temporally from a deeply cupped optic disc. The temporal and nasal extensions of this band fade out gradually and stop completely a short distance behind the equator of the eyeball. All the fibres do not run a parallel course along the band up to its nasal and temporal extremities, but fall out of it, at various intervals, to a slight extent above and more prominently below. This band is 2 mm. wide and 7 mm. long, lying between the upper and the middle thirds of the retina. The myelinated band occupies an area of 6^{o} to 10^{o} wide in the visual field (Chievitz 1891, Davis 1929 and Thompson 1953).

The vascular system of the retina is as unique as its band of myelinated fibres. Having entered the optic nerve ventrally about 1 mm.

behind the eyeball, the arteria and the vena centralis course obliquely upward and forward to reach the centre of the papilla. The central vessels divide into nasal and temporal branches just before or just after their entrance into the optic nerve, then mount up the margins of the cup of the papilla and bend over its rim, to be distributed along the bundles of the myelinated nerve fibres, dividing and subdividing into numerous branches along its course. Outside the myelinated area, the retina is devoid of any blood vessels. It is suggested that the central arteries nourish the strongly developed myelinated band only. The other layers of the retina are, presumably, nourished by the choroidal vessels (Muller 1861, His 1880, Jhonson 1901, Davis 1929 and Sheppard 1961).

Though the rabbit's retina is not provided with a macula, there exists a sensitive area "the visual streak" as it is called, which corresponds to the pigmented streak of the choroid. It is a 3 - 4 mm. wide area which extends horizontally, its centre being located 3 mm. below the papilla. The histological appearance along this visual streak is quite different from the surrounding retina. Here the total thickness of the retina is 160 microns in contrast with the thickness of 120 microns, 36 microns and 90 microns, a short

distance above the margin of the disc, under the myelinated band and near the ora respectively. This is due to an increase of thickness of all the layers of the retina. The situation of the retinal ganglion cells appears to be controversial along this "visual streak". Though Davis (1929) claims that the ganglion cells lie in a single layer along the "streak", meaning obviously no increase in ganglion cell concentration in it, a ganglion cell count done recently in this laboratory (Seneviratne 1963) showing increased concentration of ganglion cells here is in agreement with Kraus's (1884 and 1895 quoted by Davis 1929) opinion of two to three layered arrangement of the retinal ganglion cells along the "streak". The ganglion cells are reduced to few isolated cells under the myelinated fibres (Davis 1929).

The total number of ganglion cell axons constituting an optic nerve is claimed to be 261,000 by Bruesch and Arey (1942).

The rat's retina differs essentially from that of the rabbit in not having a myelinated band and in having a concentric distribution of the ganglion cells, the centre of which, with maximum concentration of the ganglion cells, is located in the inner half of the posterior quadrant, on or just above the horizontal line that passes through the optic disc (Lashley 1932).

III THE OPTIC NERVE, CHIASMA AND OPTIC TRACT

Since approximately the middle of the last century, systematic attempts have been made to discover the organisation of the retina, in the lower animals, on the subcortical and the cortical visual centres. The weapon of attack being histological, the details of observation varied from time to time with the technique employed. The earliest authentic finding is probably that of von Gudden (1870) who, following retinal destruction in newborn rabbits, observed a thinning of the optic nerve concerned, which became grey with irregularly arranged fibres. A similar observation of recent time is that of Chase (1943) who, using erythrosin-eosin, Nissl and iron-hematoxylin stains, in the rat, observed "practically no fibres" in the optic nerve of the enucleated side, after varying periods of survival, up to one year. Atrophic changes made their appearance after three months and were exaggerated with time.

However, von Gudden's conclusion of complete chiasmal decussation, on the ground that the optic tract on the side of the injured eye showed preservance of neurilemma while its complete disappearance was observed on the other optic tract, is fallacious.

The idea of making focal retinal lesions and following subsequent degeneration by Marchi technique was utilised by Pick (1895) with Herrenheise, who observed, in the rabbit, that the degenerated fibres retained their respective retinal position up to the chiasma, where they decussated, and interchanged their position, mediolaterally only, in the contralateral optic tract. Their reticence regarding the uncrossed fibres in the optic tract could be explained by their restricting the lesions too near the optic disc. This point was elucidated by Loepp (1911-12) in his Marchi-study following unilateral enucleation in the rabbit. In his opinion the small group of fibres that escape chiasmal decussation are intermingled with the crossed fibres from the opposite side, in the optic tract. Similar observations about the uncrossed fibres, following unilateral enucleation, were made in the rabbit's Nissl preparations of Minkowski (1919) and in the opossum by Bodian (1935) with the help of Marchi technique. This intermingling of crossed and uncrossed fibres was denied, in Marchi prepared rabbits by Brouwer (1923) and rats by Lashley (1934a).

However Pick's erroneous statement regarding the upper and lower retinal fibres

maintaining their identical position in the contralateral optic tract was rectified by Brouwer (1923) in his Marchi-prepared rabbits following restricted retinal lesions.

Following the same operative procedure and histological technique as Pick, Usher and Dean (1896) observed a number of rabbits which ratified Pick's view so far as optic nerve was concerned. However, merit of Usher and Dean's communication lies elsewhere. They observed denser degeneration by dividing the myelinated band than by making lesions in the peripheral retina. Such results are not unexpected, especially from lower myelinated band lesions which involve the "visual streak" and cause destruction of more axons originating from the retinal ganglion cells. Their observation of minute black dots in the healthy optic nerve could be discarded as an artifact, since such artifacts are not uncommon in Marchi technique.

In the rat's optic tract Lashley (1934a) observed a somewhat similar distribution of retinal fibres. He states that for the most part the degeneration from the peripheral (retinal) lesions is concentrated in the lower (caudal) part of the optic tract and when the lesion is near the disc degeneration appears

"throughout the hight of the tract". Though the reason for the first part of the statement remains obscure, a suitable explanation for the second part is not difficult to proffer. A scrutiny of his protocol reveals that all his effective central lesions (that is, those that are said to be near the optic disc) are temporally situated. As the fovea in the rat is also temporally placed (Lashley 1932) such lesions can easily damage the fovea or at least the papulo-macular bundle (as the rat is expected to have one) and cause more diffuse degeneration.

The Accessory Optic Tract: von Gudden (1870) following unilateral enucleation in different mammals observed atrophy of a small bundle of fibres besides that of the optic nerve and the primary optic centres. He called this small bundle "Tractus Peduncularis Transversus". In 1881, following the same procedure, only in the new born rabbits, he established the existence of this tract. This tract is said to emerge from the superior quadrigeminal brachiumand to course over it to its rostral edge. It then passes over the surface of the inferior quadrigeminal brachium, on to the surface of the cerebral peduncle. From there

it could be followed round the cerebral peduncle to its medial edge. The existence of the accessory optic fibres has since been confirmed by different observers, in rabbits (Berl 1902, Loepp 1911-12, Giolli 1961), in the rats (Lashley 1934a, Chang 1936, Tsang 1937, Hayhow, Webb and Jervie 1960) and in the opossum (Tsai 1925).

IV THE LATERAL GENICULATE BODY

1. ANATOMICAL DESCRIPTION OF THE LATERAL GENICULATE BODY

In their description of the rabbit's lateral geniculate body, Winkler and Potter (1911) state that most anteriorly this structure can be divided into dorso-medial and a ventro-lateral ganglia separated by a lamina medullaris. The dorso-lateral ganglion covering the nucleus reticularis is bordered medially by the nucleus lateralis of the thalamus and is covered on its lateral side by the fibres of the optic tract. The dorso-medial nucleus is composed of small round cells. The ventro-lateral nucleus is triangular in shape with its apex pointed ventrally to the optic tract. This nucleus, in turn, is subdivided into two parts, the lateral part being composed chiefly of fibres from the optic tract with large cells scattered in it. The medial part is composed of small multipolar and pyramidal cells. Further posterior, the dorsal nucleus attains a considerable size with its small cells arranged in rows separated from each other by the fibres that enter the nucleus from its dorso-lateral side. In a subsequent paper Winkler (1918) makes further distinction in the arrangement of the cells in this nucleus.

It is only in the dorsal part of the nucleus this stratification, caused by the incoming fibres, is noticed. He calls the stratified segment - "part a" of the dorsal nucleus. The ventral segment of the dorsal nucleus is devoid of any stratification, the reason being, the fibres, having gained their entrance from the dorso-lateral side of the nucleus, have to travel the whole transverse thickness to reach the ventral segment. In doing so they lose their own regular arrangement and fail to organise the cells of this segment in any definite order. Winkler calls this segment - "part b" of the dorsal nucleus. The stratification and its cause is in agreement with Glees' observation (1941-42).

Though Winkler and Potter (1911) and Winkler (1918) suggest only one type of cells in the dorsal nucleus of the lateral geniculate body Koelliker (1896) on the other hand claims existence of cells of two distinct types. The large solitary "Strahlenzell" with recurrent collaterals and small "Buschzell" which occur in clusters.

In the Virginian opossum the type and size of the cell population of the dorsal nucleus of the lateral geniculate body is consistent with

those of the rabbit's dorsal nucleus as observed by Koelliker. In this animal, the dorsal nucleus is composed of numerous large multipolar and star shaped cells with big nuclei and scanty small round and pyramidal cells (Tsai 1925). These large and small cells are not definitely organised. A group of small cells ventral to and separated from the dorsal nucleus constitute the ventral nucleus of the lateral geniculate body in the opossum.

A similar variety of cells is claimed by Waller (1934) for the dorsal nucleus of the lateral geniculate body in the rat. Though the cells, in general, are of medium size and quite sharply outlined, containing granules, those of the superficial or the dorsal half of the nucleus are larger than the ventro-medial half.

2. THE RETINAL REPRESENTATION IN THE LATERAL GENICULATE BODY

The establishment of retinal connection in the dorsal nucleus of the lateral geniculate body dates back to 1870, when von Gudden, following unilateral enucleation in the rabbit, observed degeneration of this nucleus by carmine stain on the contralateral side. This was confirmed by Loepp (1911) in the same animal

with the help of Marchi technique. In Loepp's opinion the arrangement of the optic fibres is not identical all over the dorsal nucleus of the lateral geniculate body. On the contralateral side these fibres are primarily concentrated over the lateral side of the dorsal nucleus and also along the boundary between it and the ventral nucleus, whereas, on the ipsilateral side the optic fibres end only in the ventral part of the dorsal nucleus, together with a small number of the crossed optic fibres. It is difficult to assess the extent of ipsilateral representation from his paper, as his free-hand drawing of ipsilateral dorsal nucleus shows a band of degeneration extending right across the whole transverse thickness of it, with clear area both above and below the band. This band obviously contains axonal as well as preterminal degeneration and Marchi is not the suitable technique for differentiating one from the other.

The extent of the contralateral dorsal nuclear degeneration, in the rabbit, is not quite the same as above in Minkowski's (1919) Nissl stained preparations. Following unilateral enucleation the degenerated area is located up to the caudomedial part of the dorsal

nucleus. This degenerated area maintains contact with the secondarily degenerated optic tract fibres of retinal origin. In his opinion the caudomedial part of the dorsal nucleus of the lateral geniculate body receives the uncrossed ipsilateral fibres, unlike ventral part as observed by Loepp.

A more precise localisation of the contralateral retinal quadrants is demonstrated by Brouwer (1923), Brouwer, Zeeman and Houwer (1923) and Brouwer and Zeeman (1926), in the rabbit. Following restricted retinal lesions they observe subsequent degeneration in the dorsal, nucleus by Marchi technique. In their opinion the upper retina is more ventrally represented than the lower and the nasal retina temporally. That is, upper nasal, lower nasal, upper temporal and lower temporal retinal quadrants are represented on the lower temporal, upper temporal, lower nasal and upper nasal parts of the dorsal nucleus respectively. The demarkation line between any two quadrants is not strictly vertical or horizontal. The temporal retinal quadrants that are represented on the nasal side of the dorsal nucleus are observed to occupy a larger area of the nucleus than the temporally represented nasal retinal

quadrants. The planes of separation of the quadrants are sharp and clear-cut and there is no overlap between the two adjacent quadrants. The uncrossed retinal fibres that accompany the lower temporal retinal fibres in their passage through the optic tract end, presumably, in the upper nasal quadrant of the nucleus, together with these fibres. Overbosch's observation, in 1926 (quoted by Lashley 1934a), in the rabbit is identical with the aforementioned works; the only point of difference being considerable overlap between any two areas of retinal representation.

In the rat Lashley (1934a) following Marchi technique observes quadrantic representation of the retina on the dorsal nucleus of the lateral geniculate body, to be similar to that of the rabbit. However, Hayhow, Softon and Webb (1962) by Nanta-Gygax stain point out that, though most of the dorsal nucleus is represented by the contralateral eye, a small area on the medial part shows distinct vertical lamination, representing the crossed and uncrossed retinal fibres, with considerable overlap.

The polemic issue of the ventral nucleus of the lateral geniculate body's acting as a subcortical centre for the retinal fibres has

its supporters and refuters. The following are the authors who are in favour of its being so: Loepp (1911-12), Minkowski (1919), Brouwer (1923) in the rabbit (both for crossed and uncrossed fibres), Tsai (1925) in the opossum, and Hayhow, Softon and Webb (1962) in the rat.

In the Virginian opossum, which has a non-laminated dorsal nucleus of the lateral geniculate body, Marchi preparations following localised retinal lesions show that the dorsal and the ventral segments of the lateral geniculate dorsal nucleus are monopolised, unlike the rabbit, by the temporal and nasal retinal representation respectively. The ventral part of the dorsal nucleus shows exclusive contralateral lower nasal retinal representation anteriorly and that of the upper nasal posteriorly. The temporal half of the retina is represented on the dorsal segment, wholly bilaterally. The lower ipsi- and contralateral temporal retina are represented anteriorly and upper ipsi- and contralateral retina posteriorly, with predominance of the ipsilateral representation on the medial side. This extensive binocular representation could well be due to the greater proportion (20%) of the retinal fibres remaining uncrossed (Bodian 1937). Besides the primary retinal

connection, Tsai (1925) claims additional connections for the lateral geniculate body with the tectum (tecto-thalamic tract) and association fibres with the nuclei lateralis and ventralis thalami.

3. TERMINAL ARBORIZATION OF THE OPTIC FIBRES IN THE LATERAL GENICULATE BODY

The terminal arborization of the optic fibres in the lateral geniculate body was observed by Cajal (1911) in great detail with the help of Golgi stain. In the new-born rabbit individual optic nerve fibre end in 'brush-like' terminals. These terminal fibres are called free-endings as they do not show any definite end formation. The dendrites of the geniculate body cells and the optic nerve fibres form a very dense neuropil in the adult rabbit. A contrary view is put forward by Cattanio (1923, quoted by Glees 1941-42). He observes that several days after the section of the optic nerve, very fine geniculate fibres show little rings and bulbs at their ends. In agreement with Cattanio's view, Glees (1941-42) observes by toludine blue, Hortega's and Bielschowsky-Gros method numerous terminal loops and rings in contact with the nerve cells and their dendrites in the normal lateral geniculate

body of the rabbit. The reason he does not mention end bulbs, like Cattanio, is he examined normal material (unlike Cattanio). The number of terminals in contact with the cell body is estimated to be ten, and many more in contact with the dendrites; the incidence of overlap is considerable. He does not specifically mention whether such enormous convergence is uniform throughout the dorsal nucleus of the lateral geniculate body or localised to any particular sector or varied from sector to sector. For, from the observations of Brouwer et al (1923a, 1923b and 1928) of unequal spatial distribution of the four principal retinal quadrants, one would expect a variation in this retino-geniculate convergence.

4. DEVELOPMENT OF THE LATERAL GENICULATE BODY

Rose (1942), using Cresylviolet staining of the 15 microns sections of the rabbits embryo, at different stages of its development, observes that from the pro-nucleus of the dorsal lateral geniculate body the definitive dorsal lateral geniculate body originates quite early in the intra-uterine life. Its origin and subsequent development is dependent on the telencephelon. Thalamic area in the early developmental stage consists of a wide matrix and a narrow mantle

layer formed by regularly arranged cells. This mantle layer is separated from the matrix by a distinct intermediate layer, almost without any cells (Zona limitance). The mantle layer soon widen greatly, the zona limitance becomes indistinct and at the same time the matrix becomes more and more exhausted. Finally in an embryo of 35 mm. length, the matrix is entirely exhausted and the whole area is almost uniformly built. After the exhaustion of the matrix, the mantle layer breaks up into a large transitional pattern-stage of pro-nuclei which finally differentiate into the definitive nuclear groups.

V THE SUPERIOR COLLICULUS

1. ANATOMICAL DESCRIPTION OF THE SUPERIOR COLLICULUS

Anatomical lamination in the superior colliculus, contrary to the dorsal nucleus of the lateral geniculate body, is obvious. The layers that acquire myriad designation from different authors can be harmonized and briefly described under the following headings. From above downwards these are:-

The first layer: a narrow fine fibre zone at the outer border with an incomplete row of cells (Huber and Crosby 1943), corresponds to the Stratum zonale of Ramon y Cajal (1911) and Winkler and Potter (1911) for the rabbit and of Tsai (1925) for the opossum, ausere Lage of von Koelliker (1896) for the rabbit and the Stro marginale of Castaldi (1923 quoted by Huber and Crosby 1943) for the guinea pig.

The second layer: composed of medium and small sized cells of oval and pyramidal shape and multipolar in character, with intermingled fine fibres from the neighbouring strata (Huber and Crosby 1943) corresponds to die ausere grave Lage of von Koelliker (1896) for the rabbit, the stratum griseum superficiale of Winkler and Potter (1911) for the rabbit and of Tsai (1925) for the opossum, zone cenree of Ramon y Cajal

(1911) for the rabbit and cappa cineria of Castaldi (1923 quoted by Huber and Crosby 1943) for the guinea pig.

The third layer: composed of medullated optic tract fibres with a fairly large number of inter neurons (Huber and Crosby 1943) corresponds to die mittlere weisse Lage of von Koelliker (1896) for the rabbit, the Stratum medullare of Winkler and Potter (1911) and the zone des fibres optque of Ramon y Cajal (1911) for the rabbit, the stratto ottico of Castaldi (1923 quoted by Huber and Crosby 1943) for the guinea pig and the Stratum opticum of Tsai (1925) for the opossum.

The fourth layer: consists of somewhat deeply stained neurons often arranged in groups of fibreous fasciculi which in part are fine and plexiform in arrangement (Huber and Crosby 1943) corresponds to the mittlere grave Lage of von Koelliker (1896) and the Stratum griseum intermedium of Winkler and Potter (1911) for the rabbit, the strato bianko cinero superficiale of Castaldi (1923 quoted by Huber and Crosby 1943) for the guinea pig and the stratum griseum mediaus of Tsai (1925) for the opossum.

The fifth layer: is a broad band of fibres interspersed with small and medium sized cells. The fascicules of the fibres are both medullated

and unmedullated (Huber and Crosby 1943), correspond to the inner weisse Lage of von Koelliker (1896) and the Stratum medullare intermedium of Winkler and Potter (1911) for the rabbit, the strato sensitivo ascendeti of Castaldi (1923, quoted by Huber and Crosby 1943) for the guinea pig and the stratum album medius of Tsai (1925) for the opossum.

The sixth layer: is a fairly wide band composed of cells of small and medium size. It also contains a layer of multipolar pyramidal neurons with intervening fibre-plexus and fibres of passage. (Huber and Crosby 1943) corresponds to the inner grave Lage of von Koelliker (1896) and the stratum griseum profundum of Winkler and Potter (1911) for the rabbit, the strato bianco cinereo profundo of Castaldi (1923, quoted by Huber and Crosby 1943) for the guinea pig and the stratum griseum profundum of Tsai (1925) for the opossum.

The seventh layer: is composed of closely arranged parallel bundles of fibres of both efferent and commissural type (Huber and Crosby 1943) corresponds to Stratum medullare profundum of Winkler and Potter (1911) for the rabbit, the strato midollo profundo of Castaldi (1925, quoted by Huber and Crosby 1943) for the guinea pig and the stratum album profundum of Tsai (1925) for the opossum.

The eighth and the ninth layers: are composed of small and medium sized cells, some arranged in rows and intermingled fibre bundles with fascicules deep to them. The fibres are thinly medullated or unmedullated. These are known as the Stratum griseum periventriculare and the Stratum fibrosum periventriculare. (Huber and Crosby 1943). These layers correspond to the grigio centra and strato germinativo of Castaldi (1923, quoted by Huber and Crosby 1943) for the guinea pig.

2. CONNECTIONS OF THE SUPERIOR COLLICULUS

The Strum zonale is a narrow band containing fine fibres which turn down into the underlying grey. According to Huber and Crosby this contains corticotectal fibres in many mammals including the rabbit. This is in disagreement with Loepp (1911-12) and Brouwer (1923) who observed degeneration of this layer after complete and restricted destruction of the monocular retina, in the rabbit.

The Stratum griseum superficiale is frequently broken down by numerous corticotectal fascicules, among which lie the small sized cells. It varies in thickness in different animals and in different parts of the retina of the same animal.

The stratum opticum contains fibres from

the optic tract and corticotectal pathway. From this stratum optic collateral may enter the overlying grey but the fibres turn downwards.

The stratum griseum intermediale, the stratum album intermediale and the stratum griseum profundum represent receptive and collateral areas for certain of the ascending system (such as the spino tectal tract) to the optic tectum and the terminals of the optic system. They also constitute an area of reception for the internal opticotectal tract from the occipital region of the hemisphere.

The stratum album profundum is composed chiefly of efferent and commissural fibres. The bodies of the neurons giving rise to these efferent fibres are situated on the overlying stratum griseum profundum, the stratum griseum intermediale and in the underlying stratum griseum periventriculare. (Huber and Crosby 1943).

3. THE RETINAL REPRESENTATION ON THE SUPERIOR COLLICULUS

Loepp (1911-12) observed, by Marchi technique, degeneration, following unilateral enucleation, on both the contra- and ipsilateral superior colliculus. The degeneration of the contralateral side includes all the layers of the

superior colliculus up to the stratum zonale, whereas that on the ipsilateral side extend only up to the middle of this structure. On the contralateral side, the upper nasal part of the retina is represented caudally on the colliculus, and lower temporal orally, lower nasal and upper temporal retinal quadrants are on the medial and lateral sides respectively. (Brouwer 1923).

VI THE VISUAL CORTEX

1. ANATOMICAL DESCRIPTION OF THE VISUAL CORTEX

The cerebral cortex of the rabbit is lissencephalic in nature, with slight convolutions. It is devoid of any deep fissures, excepting a shallow antero-posteriorly orientated sulcus on its postero-medial aspect approximately 2 mm. from the midline, called the fissura sagittalis lateralis or the splenial sulcus (Brodmann 1909, Bishop and O'Leary 1936, Thompson, Woolsey and Talbot 1950, and Duke-Elder 1958).

The extent of the visual area of the cortex was cytoarchitectonically determined, in the rabbit, by Brodmann (1909). Following his six layer plan for the cortex, he observed that in the visual area, layers IV and VI were divisible into three sublayers in each, of which layer IVb - "L. granularis interna intermedia" contained the stria of Gennari or the white line. In his opinion area 17 on the main visual area was approximately triangular in shape with its apex directed towards the posterior pole of the cortex. Area 17 was bordered by a narrow ribbon-like area 18 along its medial and postero-lateral margins only. A small extension of the area 18 was observed

to encroach upon the medial side of the hemisphere at the level of the posterior pole of the cortex. The lack of uniformity in cell arrangement in the area 18 was the distinguishing feature, in his opinion, between it and the area 17. A more detailed and complicated cytoarchitectonic map was provided, years later, by Rose (1931), following six layer plan of Brodmann (1909). The extension of his striate area approximately corresponds to the area 17 of Brodmann. The significant difference lies in the distribution of peri- and para-striate areas, which presumably correspond to area 18 of Brodmann. In Rose's map, the medial side of the dorsal surface of the striate area is bordered by the peri-striate area which lies along the fissura sagittalis lateralis, between the striate and the area retrosplenialis granularis dorsalis. Anteriorly the striate area is bordered by the para-striate 3 and the para-striate 4 areas. The lateral and the posterior margins are devoid of any para- or peri-striate fringe. Another distinguishing feature in Rose's map is the small extension of the visual area on to the medial surface of the hemisphere. He claims it to be an extension from the striate area, contrary to Brodmann's suggestion of its being area 18.

The layers in the striate area are narrow in general. Layers II and III contain tightly packed small cells. The lamina granularis (IV) is broader, more on its inner part than the outer. The relatively narrow lamina ganglionaris (V) is densely populated by cells on its outer part, the broad lamina multiformi (VI) is thinly populated by cells on its outer part. The peri-striate area differs from the striate in possessing a broader zonal layer (I) and thinner layers II, III and IV. Lamina ganglionaris (V) of this area is identical, in cell distribution, with that of the striate area whereas the lamina multiformi (VI) is relatively narrow.

O'Leary and Bishop (1938) undertook a detailed histological study of the rabbit's visual cortex following Nissl and Golgi-Cox stain of normal material. A summary of their observation is given below. The constituent layers are described in sequence from above downwards.

I Plexiform layer: is 20 microns thick. It is populated by neuroglial cells, though invasion by the pyramidal cells of layer II is not uncommon. Horizontal cells of Cajal, with axonal arborization confined to this layer may also be seen.

II and III Layer of modified pyramidal cells and layer of small and medium sized pyramidal cells: These layers are moderately densely populated with large and small cells of 10 microns to 15 microns diameter; that of the largest is 20 microns and the smallest 5 - 10 microns. These cells are scattered throughout the layers. The upper quarter of layers II and III is populated by small round or angular cells and the lower three-quarter by pyriform cells with oval nuclei. In addition cells with conoid bodies and basket-like terminals, cells with conoid or polyhedral bodies and extended basal dendrites, polyhedral cells with multipolar dendrites, moderately large conoid or fusiform cells with thick axons are also seen in these layers. All pyramids of layer II appear to have slender vertically descending axons, issuing lateral branches as they pass through layer III. The majority of the vertically descending axons of layer III reach the basal white matter.

IV Layer of granules: is populated by small cells of 4 microns to 8 microns diameter, sharply demarcated towards layer III and mingling with cells of layer V. The cells of this layer have pyramidal fusiform or polyhedral bodies; as their axons descend vertically, collaterals are seen to branch off, which are

mostly confined to the same layer. Fusiform cells with polar dendrites of vertical extension and vertically directed axons, small ovoid cells with bipolar dendrites and ascending axonal arborization, conoid cells with multipolar and ascending axons, polyhedral multipolar cells with horizontal axons, goblet cells with laterally extended dendrites and ascending axons and small conoid cells with multipolar dendrites and ascending axons are also seen in this layer.

V Layer of large pyramids: The main type of cells is the large pyramidal cells of sublayers Va and Vb, with smaller cells in between them. The large pyramids are 20 microns to 30 microns in diameter with ascending dendrites to the plexiform layer and basal dendrites whose distribution is mostly confined to layer V or very occasionally may pass through layers V and VI to the white matter. Additional cells of various size and shape with short axons are also present.

VI Layer of Polymorph cells: The principal cells constituting this layer are pyramidal cells of small or medium size. Multipolar or ovoid cells with scanty cytoplasm may also occur. The basal dendrites divide and proceed laterally and the apical dendrites ramify in the plexiform layer.

Regarding the axonal termination of the afferent fibres O'Leary and Bishop (1938) are of opinion that the coarse axons proceed upwards from the white matter, without branching to the lower margin of layer IV, here, sometimes after issuing lateral branches, they appear to divide dichotomously and proceed upwards through the layer of granules (IV). They do not terminate entirely in layer IV but enter layer III, continuing to subdivide on their way.

2. CONNECTIONS OF THE VISUAL CORTEX

One of the earliest attempts to establish precise cortico-thalamic connections, in the rabbit, is probably that of von Monakow (1881) who observed, by carmine stain, complete degeneration of the lateral geniculate body following total visual cortical lesion. It is not clear from his paper whether he observed the retrograde degeneration to be confined to the dorsal nucleus of the lateral geniculate body only. Besides this, he also observed complete degeneration of the internal capsule and outer part of the peduncle and tentative degeneration of the reticular formation of the same side.

Years later Winkler (1918) designed his experiments with more elegance. He followed retrograde degeneration subsequent to restricted

visual cortical lesions, in the rabbit, by Marchi method. He observed atrophy of 'part a' of the dorsal nucleus of the lateral geniculate body following postero-lateral cortical lesion, atrophy involving portions of 'part a' and 'part b' following postero-medial cortical lesion, atrophy of ventral segment of 'part b' and dorsal segments of 'part a' and 'part b' following antero-lateral lesion and atrophy of the 'part b' only following a lesion more medial to the first one. Though his observations are not informative enough to construct a retinal representation map, still they show that some sort of spatial organization for the different retinal areas is possible on the visual cortex. Besides the heavy cortical scarring following lesions, as shown in his illustrations, makes one feel that he might have made wounds deep enough to disturb the radiation fibres destined to areas other than the area of lesion.

However, a deliberate attempt to produce a more comprehensible and precise map of the visual cortex of the rabbit was made by Putnam and Putnam (1926). Having Brouwer's map of retinal representation for the rabbit's lateral geniculate body, to guide them, the Putnams made localized cortical lesions and followed the degeneration by Marchi, to the dorsal nucleus of the lateral

geniculate body. They state that the nasal quadrants of the retina are projected on the postero-inferior sectors of the striate cortex and the temporal retinal quadrants on the antero-superior. The superior retinal quadrants are superiorly placed on the cortex and the inferior retinal quadrants inferiorly. The ambiguity of superior and inferior cortex is elucidated by their illustration, which shows nasal retina postero-laterally, temporal retina antero-medially with superior and inferior segments medially and laterally respectively. The binocular projection is represented by a antero-medial protrusion of the visual area bordering the whole of the temporal representation.

The observation of Waller (1934) on the rat by Nissl stain that total visual cortical lesion produced complete degeneration of the dorsal nucleus of the lateral geniculate body, while partial medial and temporal cortical lesions produced deeper and superficial atrophy of the dorsal nucleus, was ratified and extended by Lashley (1934b) by Marchi following localized lesions. Lashley observed that, in the rat, temporal retinal quadrants were projected laterally the medial quadrants medially with lower and upper quadrants

anteriorly and posteriorly. The binocular field is represented antero-laterally on the cortex. In his opinion cortico-geniculate association is very precise and approaches a point-to-point correspondence.

In the opossum a greater cortical area is devoted to the binocular projection. It covers the whole of the temporal side of the cortex, the upper temporal retina being anterior and lower temporal posterior, the nasal retinal quadrants are projected medially with the upper nasal, as expected, anterior (Bodian 1935,37). Though this map resembles more closely that of the rat by Lashley, Bodian, for some obscure reason claims its correspondence to that of the rabbit by the Putnams, which, in fact, it does not.

A localized cortico-geniculate connection in squirrels has been made by Vaidya (1962) by studying chromatolytic changes in the lateral geniculate body and the gliosis following localized cortical lesions. He finds the medial two-thirds of the posterior half of the dorsal surface of each hemisphere has geniculate connections and calls it visual cortex. He finds only four layers in it. The dorsal pole of the lateral geniculate body is projected on the medial part of the cortex, the ventral part on

the anterior-lateral sector and middle segment of the lateral geniculate body on the postero-lateral sector. He does not claim any representation for the retina on the visual cortex, probably, as the retinal representation on the lateral geniculate body in the squirrel is not known.

Inter cortical connections was studied, in the rat, by Krieg (1947 by Marchi) following localized lesions in one visual cortex. He states that, callosal connection between two areas I7 - does not exist.

According to Krieg area 18 which is medial to area 17 (Krieg 1946) has a doubtful callosal connection through the posterior extreme of the splenium. Besides area 18 has reciprocal connection with area 17 and area 18a (located lateral to area 17, Krieg 1946). On the contrary Nauta and Bucher (1954) deny any callosal connection of area 18. They are of opinion that the callosal fibres originate in all parts of the striate area, only the lateral part of the striate area and an adjoining part of area 18a appear to receive such connections and transmit them through the corpus callosum to the same area (lateral area 17 and adjoining 18a) of the opposite hemisphere. The intrinsic

associations among areas 17, 18 and 18a are more diffusely organized.

INTRODUCTION

B. ELECTRO-PHYSIOLOGICAL STUDIES

1. THE VISUAL CORTEX

In Granits opinion electro-physiology of the higher visual centres only "... served to confirm and extend anatomical knowledge". This harsh remark, made in 1962, is not justified. For a considerable amount of electro-physiological study, on cats and monkeys particularly, has been done by 1962, which is not restricted to confirmation of the anatomical knowledge. However, the electro-physiological studies of the rodent in general and the rabbit in particular does not seem to be as popular as that of the higher mammals. The cortex, in the rabbit, attracted attention of the physiologist first; presumably it was easier to approach. Though primarily concerned with the nature of the cortical response to visual stimulation, some assessment of the extent of the visually excitable cortical area was undertaken by them.

Bartley and Bishop (1933a) noticed, by stimulating the optic nerve following enucleation and recording with silver and silver chloride surface electrode, that, on the contralateral visual cortex of the rabbit, specific response to stimulation was confined to the posterior half; the medial boundary of this visually excitable area was limited by the sulcus lateralis sagittalis. The response to contralateral

optic nerve stimulation was superimposed upon the waves of spontaneous activity of the cortex. The evoked response consisted of two components - one small monophasic response to weakest stimulation and a second diphasic response following a stimulus of slightly higher threshold. By varying the time-interval between the stimuli a series of at least three small waves following the monophasic wave was observed. These two sets of responses were assumed to be due to a separation in the visual cortical pathway in the thalamus. They assured themselves of the visual cortical origin of the spontaneous activity by observing a depression of this activity in the refractory phase following direct stimulation of isolated areas of cortex, in the devascularized patches of cortex and by observation of a comparable depression of spontaneous activity with other reflexes under deep anaesthesia (Bartley and Bishop 1933b).

Following application of strychnine under the surface electrode an increase in the diphasic wave and a decrease in the spontaneous activity was observed after optic nerve stimulation; also a spread of the cortical activity to the neighbouring area "in course of time"(Bartley 1933). By applying "strong"

stimuli to the rabbit's optic nerve and simultaneously activating many fibres thereby, Bishop (1933) came to the erroneous conclusion that the projection pathway from one point of the retina to the corresponding point of the cortex was multiple and subjected to influence of impulses over other similar pathway. The influence of intensity and duration of the stimulating light, flooding the whole eye, on the "implicit cortical time" or the latent period, was studied by Bartley (1934). A short latency following increased duration and intensity of the stimulus was observed.

Bishop and O'Leary (1936), in their attempt to improve upon Bartley and Bishop's (1933a) vague localization of the visual area of the cortex, investigated rabbits using steel surface and penetrating electrodes insulated up to 1 mm. of the tip, with celluloid cement and stimulating the optic nerve directly. They stated that the region from which visual responses could be obtained was roughly oval in shape, extending from the posterior pole 12 mm. to 15 mm. anteriorly. They tentatively included the lateral sulcus and an area "slightly medial" to it within the visual cortex. From its medial boundary the visual area extended 10 mm. to 12 mm. laterally. The boundary between the

visually active and inactive area varied by 2 mm. or so from rabbit to rabbit. A precise correlation between histology and electro-physiology was achieved by O'Leary and Bishop (1937), regarding the lateral boundary, using penetrating electrodes during experiment and subsequent histological examination to check up the position of the electrodes from which visual response was obtained on the lateral side. In their opinion, though the histological lateral boundary of the striate area coincided with the functionally defined limit of the optically active area, a histological transition zone of 1 - 2 mm. wide, occupying the striate area and the area occipitalis of Rose (1931), could not be assigned exclusively to either field (areas). This transitional area showed a "minimal" visual response. The anterior boundary of the visually active area extended through the regions marked Para 3 + str by Rose, and in some brains may enter area Para 3. (O'Leary and Bishop 1938 and O'Leary 1938).

Talbot, Woolsey and Thompson (1946) and Thompson, Woolsey and Talbot (1950) sought for more accurate information on the retinal projection of the visual cortex on the cortex of the rabbit. They claim that the visual area extends for 15 mm. postero-anteriorly from the

posterior pole of the cortex and from 1 - 2 mm. medial to the sulcus lateralis to halfway down the lateral surface of the brain. They divide the visual cortex into a postero-medial area I and an antero-lateral area II, one being the mirror image of the other. The binocular projection is represented by a band occupying both the areas I and II partially. The vertical meridian of the binocular vision is situated 20 degrees from the sagittal plane of the visual field of the deeply anaesthetized animal and when projected on the cortex divides the binocular area into approximately equal halves. The area II is rather smaller than the area I. The upper visual field (inferior retina) is represented on the lateral cortex and the lower fields (upper retina) medially. The nasal visual field (temporal retina) anteriorly and the temporal visual field (nasal retina) posteriorly in visual area I. The projection on the visual area I is in near agreement with the Putnams histological work. This makes one wonder whether Walls' (1953) calumny about the Putnams and Brouwer is justified. Besides Walls seems to be too concerned with the idea of visual area II to pay any attention to the projection of individual retinal quadrants on the cortex.

Spectral sensitivity of the anaesthetized rabbit's visual cortex and retina was studied by Monier, Schwarz and Jordan (1962). The retinal spectral sensitivity, which is maximum at 498 m.microns with steeper and deeper fall towards the long wave length, corresponds, in their opinion, to the absorption curve of rhodopsin. The visual cortical spectral sensitivity follows that of the retina faithfully. The spectral sensitivity curve and absence of Purkinje-shift lead them to postulate, contrary to Davis' (1929) view, that the rabbit's retina consists mainly of rods, and the rabbit perceives, chiefly, variation in luminosity.

2. THE LATERAL GENICULATE BODY

Recording from the rabbit's lateral geniculate single units, Arden and Lu (1960a and 1960b) observed two main types of responses. The usual response being a brief burst, at the onset of the stimulation, followed by a long silent period, which in turn was followed by a delayed burst. The second type was a continuous burst with a long train of spikes, throughout the period of illumination. This is in consistent with Thompsons observation from the optic nerve. They attribute this variation in

response to the two types of cells observed by Koelliker (1896). In the lateral geniculate high frequency discharges are evoked both in light and in darkness. This resting discharge can be inhibited by flicker.

Existence of the extra-retinal input in the rabbits lateral geniculate body was observed by Arden and Soderburg (1961). They state that the lateral geniculate body receives afferents from the brain-stem reticular formation system, as the resting discharge which persists in the encephale isole preparations, is abolished in cerveau isole. Retinal afferents are said to be inhibitory to this input system as the discharge increases after the retinal afferents are cut-off by artificially raised intra-ocular pressure. Besides the reticular formation inputs, afferents from the auditory system are said to evoke responses in the lateral geniculate body.

The units that are dependent on the retinal input are principally divided into simple and complex (Arden 1962, 1963a, 1963b). The simple units have a slightly irregular or oval fields, showing both excitatory and inhibitory phenomena, the response being uniform throughout the field without 'centre' and 'surround' effect. The average size of the fields is 6 degrees. The complex units vary

greatly in size of the field and nature of response. Some of the complex units are as large as 80 degrees where the response changes "several times from off - to on - and back again"! Units with vertically orientated narrow fields and fields showing movement sensitivity, with directional preference are also common. The complex fields are ascribed to the overlap of retinal inputs.

Spectral sensitivity of the lateral geniculate body of the rabbit, as observed by Hill (1963) shows a maximum between 500 m. microns to 510 m.microns by the excitatory units whereas inhibitory units are most sensitive to 400 m.microns to 450 m.microns.

3. THE RETINA, THE OPTIC NERVE AND THE ACCESSORY OPTIC SYSTEM

The behaviour of the single units at the retinal level is somewhat different from those of the lateral geniculate body. Thompson's (1953) observations of single optic nerve of the rabbit reveal two main types of responses - those responding only at the commencement and cessation of light stimulus, that is, responding only at 'on' - and 'off' -, and the others which show a maintained activity throughout the period of illumination, in addition to bursts at

the commencement and the cessation. The ratio of the first and the second type of responsesis 4:1. Thompson at one stage observed response from a wide retinal area which he ascribed to scattering of light due to those rays which fall on the myelinated band. In his opinion the average field of a single ganglion cell is "somewhat larger than 1 mm."

Barlow and Hill (1963) in their observation of single unit behaviour of the rabbits retinal ganglion cells state that in addition to concentric 'on' - and 'off' -, with centre and surround, some of the retinal ganglion cells show directional selectivity to movement. These units have a diameter of 5 degrees and respond to both commencement and cessation of light stimulus. The presence of concentric fields at the retinal level is unique because, at the lateral geniculate level, they are not observed by Arden.

Hamasaki and Margi (1962) recording from the nucleus of the trans-peduncular tract show the usual 'on' - 'off' - and "on and off" units. They find these units quite well organised; the "on-off" units are dorsally placed and are attributed to the large dorsal group of cells, whereas the 'on' and 'off' responses are ventrally placed and are probably

due to small closely packed ventral cells.

They observed the configuration of the whole receptive field to be a horizontally oblong area of the central visual field.

4. THE SUPERIOR COLLICULUS

The electro-physiological mapping of the superior colliculus of the rabbit, pioneered by Hamdi and Whitteridge (1953) and completed by Kerr and Seneviratne (1963) and Seneviratne (1963) shows that the visual field represented on the collicular surface of the anaesthetized rabbit is of the shape of a narrow band. It extends horizontally through almost 180 degrees, but its maximal vertical extent is not more than 40 - 50 degrees. This band shaped projection is tilted, so that the peripheral extension of the posterior field is confined between 0 - 30 degrees meridians and that of the anterior field is between the 180 - 200 degrees meridians. The horizontal extent of the band is projected along the antero-posterior axis of the colliculus with the nasal field anterior and the temporal field posterior.

Magnification factor along the vertical axis is maximum at the centre, falling rapidly at the periphery, whereas that along the horizontal axis shows remarkably little alteration with

retinal eccentricity.

Multi-unit recording from the superior colliculus shows fields of elongated shape, the size of the field increasing gradually from superficial to deep.

EXPERIMENTAL METHODS

EXPERIMENTAL METHOD

Forty-three pigmented rabbits, whose body weight ranged from 2 - 3 kg. were used in this study. The rabbits were anaesthetized by injecting, into the marginal vein of the ear, a 4.0 c.c./kg. solution of 500 mg. of chloralose and 5.0G of urethane dissolved in 25 c.c. of water. In later experiments intravenous injection of 7 c.c./kg. of 25% urethane (half of the total dose initially followed, 7 to 10 minutes later, by the remaining half) proved more satisfactory. A desirable level of anaesthesia was maintained by the second procedure for 10-12 hours, after which period a half hourly intra-peritoneal injection of nembutal (0.1 c.c. of nembutal in 1 c.c. of 0.9% normal saline) was required for satisfactory depth of anaesthesia.

After having the rabbit anaesthetized, its trachea was cannulated and the airway cleaned with a long feather from time to time.

In the earlier experiments the skin and the cartilage of the external auditory meatus of both the ears were incised to allow easy access of the ear-plugs into the bony meatus; this operation facilitated rigid fixation of the rabbit's head in the stereo-taxic holder, enormously for the rabbit's external auditory

canal ran obliquely from the cartilagenous to the bony part. This, however, induced considerable bleeding and certain amount of surgical shock. To overcome these handicaps, the skin, soft tissue, cartilage and bone were button-holed, in the later experiments, at the base of the external ear, care being taken to make the hole big enough to ensure easy entry to the slender metal ear-plugs.

Initially no particular care was taken about the eyes, besides keeping the cornea moist and clear. In the later experiments the eye that was stimulated was immobilised effectively with help of a brass ring of appropriate size, sutured under topical application of xylocaine (Lignocaine-hydrochloride) - round the limbus; a lateral canthotomy was found necessary for the introduction of the ring and its manoeuvre. The advantage that was gained, besides having the eye immobile, by the introduction of the "ring", was the ease with which the myelinated band could be made horizontal and the optic-disc to project on an identical spot in the visual field for all the experiments, which was a great help while recording from a deep-seated structure like the dorsal nucleus of the lateral geniculate body. The left eye was stimulated in mapping monocular

visual field as well as in single unit study.

The cranial vault was exposed by a cruciate skin incision. For the experiments on the lateral geniculate body a hole was bored, by a high speed dental drill, on the right dorsal surface of the skull, close to the bregma, large enough to cover the nucleus as required by the rabbit's stereo-taxic atlas of Sawyer, Everett and Green (1954). For the cortical mapping the cranial hole extended from the bregma to the lambda, antero-posteriorly, and from the sagittal suture to a point approximately on the junction of the lateral surface with the base of the skull. The soft tissue on the side of the head was removed and the mandibular processes covering the lower lateral surface of the skull was nibbled away and a wide lateral exposure achieved. Bleeding from diploe was arrested with plasticine. The exposed dura was covered with cotton wool soaked in warm liquid paraffin and the skin apposed by a suture, till the rabbit was mounted in the stereo-taxic machine. 10 - 15 c.c. of Dextran was injected, as a routine, immediately after surgery.

Body temperature was maintained at 37°C by carrying out the surgery on thermo-regulator fitted table, and by putting an electric blanket round the animal, with a rectal thermistor, during the experiment.

After having done the surgery, the rabbit was mounted in a head-holder which provided rigid fixation of the head in the intra-aural plane. A 1.5 mm. thick block attached to one end of a brass plate was placed on the lambda, with a spirit-level on the brass-plate itself, and the head adjusted, by rotating it round the axis passing through the bony external auditory meatuses, for the 1.5 mm. difference between bregma and lambda (lambda being lower) required by the stereo-taxic atlas of Sawyer et al (1954). Further rigidity was ensured by a mouth plate and nose-fixer, as shown in fig. 1(a).

For stimulating the left eye, the head-holder was so arranged that this eye was at the centre of the perimeter with the sagittal plane of the head at right angles to the axis of reference of the apparatus. Initially the eye was centred on the perimeter by observing, on the centre of the cornea, the image of an illuminated cross, placed at the point of reference of the apparatus. In the later experiments, where the "eye ring" was used, the myelinated nerve fibre band was made horizontal and the optic disc to project 18° - 20° below the centre of the perimeter, on 245 - 255 meridian, by manipulating the "ring" under visual control (a Fison Indirect Binocular

Ophthalmoscope was used after having the pupil dilated by 1% atropine-sulph. solution).

The dura was incised next and a good exposure of the cortex gained. Cortical drying was prevented by a liquid paraffin pool made by sewing the scalp round a metal ring. The liquid paraffin pool did not prevent free pulsation of the brain. Though satisfactory lateral geniculate mapping could be done in spite of this pulsation, single unit study and also cortical mapping was rendered impossible by it. In the later experiments cerebral pulsation was got rid of by the use of 4% agar-gel, which was heated to its boiling point in a water bath and then gradually cooled to a temperature of 42° - 43°C before sealing the cranial hole with it. Micro-electrodes penetrated the structureless agar-gel (Arden 1963a) with ease and impunity. Mapping of the lateral surface of the cortex required wide exposure of the lateral side skull, which was agar-sealed by turning the head in the holder for 90° through the antero-posterior axis so that the lateral-skull-hole was directed upwards. Once the agar was solidified the head was rotated back to its correct position.

Toughened Anstentic Stainless Steel

Surgeon's Intestinal needles were electrolytically polished by repeated immersion in a solution made up of

Syrupy Phosphoric Acid 42%

Concentrated Sulphuric Acid 34%

Water 24%

(Seneviratne - 1963)

6V. AC. from a mains transformer was passed through the needle and the indifferent electrode, a carbon rod, placed in the electrolytic bath. A smooth shining surface and a long even taper ending in a tip diameter of 1 - 3 microns, were the criteria of a satisfactory electrode. Individual electrode was washed in weak-alkali for 10 - 12 hours followed by plain-water washing for 5 - 6 hours, followed by 10 - 12 hours drying in a closed dust-free chamber. The dried electrodes were insulated with a coat of INSL-X-E 33N clear varnish (The INSL-X Company Inc. N.Y.). The chloroform-thinned, honey consistency INSL-X was used for the purpose, in which the electrode was gradually dipped, with the tip directed upwards, until observation through a binocular disecting microscope showed terminal 3 - 5 microns standing free from the varnish. The electrode was then withdrawn quickly from the varnish and allowed to dry

for 10 - 12 hours in a dust-free chamber. Impedance of the dry electrode was measured, in a saline bath with the help of a Heathkit 7VA Valve-Voltmeter. Measured under these conditions, electrodes of 350K to 450K ohms impedance proved satisfactory for mapping. For single unit study an impedance of 1 - 2 Mg.ohms was required. Tungsten electrodes were electro-polished in supersaturated solution Sodium Nitrite, the rest of the treatment being similar to that of the stainless-steel electrodes.

The electrode bridge of the stereo-taxic machine was provided with three micro manipulators permitting antero-posterior, side-to-side and vertical excursion of the electrode, to an accuracy of 10 microns.

In the lateral geniculate experiments, mapping the projection of the visual field, as well as single unit study, the stereo-taxic atlas of Sawyer et al (1954) was used. After having the electrode in the correct stereo-taxic plane for the thickest part of the lateral geniculate body of the right side it was lowered vertically through the brain. Recording from the hippocampus, encountered at a depth of 5 - 6 mm. from the cortical surface, proved to be an effective landmark. Responses from the dorsal nucleus of the lateral geniculate

body were recorded, approximately, 6.5 mm. below the cortical surface. In lateral geniculate body single unit study an electrolytic lesion was always made, at a known depth, by disconnecting one of the cathode follower batteries for 5 seconds, for histological identification of the part of the lateral geniculate body from which the unit was studied. The electrode was re-introduced at 500 microns intervals both antero-posteriorly and mediolaterally.

The dorsal surface of the cortex was mapped by vertically-driven electrodes whereas the lateral surface of the cortex was mapped by electrode driven from the sides, as shown in fig. 1 (b). Electrode penetrations were made at 1 mm. intervals in cortical mapping.

The activity was displayed by amplification of the voltage between the tip of the microelectrode and the indifferent electrode, buried under the scalp. A cathode follower and a three-stage R.C. coupled amplifier with variable time-constant was used; single-unit activity was photographed at a time constant of 5 m. sec. The output from the amplifier was fed in parallel to a display oscilloscope, loudspeaker and the oscilloscope of the camera unit. A second display oscilloscope carried the signals

indicating commencement ("on") and cessation ("off") of the light stimulus, being activated by the photo-cell of the perimeter. Two double beam cathode-ray tubes were included in the photographic unit; the cellular activity, stimulus signal and a time signal indicating 10 and 100 m. sec. intervals being carried on three of its traces.

The preliminary exploration of the visual field and approximate localization of a particular response, was performed by a short duration neon-flasher, triggered by the sweep of the display cathode-ray tube; exact localization of the receptive field on the perimeter arm, estimation of its shape and size was done with the 1 mm. spot-light attached to the perimeter.

A modified "Aimark" perimeter, whose arms had a diameter of 33 cm. was used. It produced white circular patches of light of 1 mm. 3 m. 5 mm. and 10 mm. in size, of approximate luminance 1.1 log foot lamberts i.e. 12.59 foot lamberts, 43.18 candela/m^2 as measured with a S.E.I. Exposure photometer (Seneviratne 1963).

At the end of the experiment the rabbit was killed with an over-dose of nembutal and perfused, through the ascending aorta, with

10% buffered formol in normal saline. After about 12 hours the brain was removed from the skull and serial coronal sections were made at 100 microns, on a freezing microtome. Frozen sections of this thickness gave satisfactory results, shrinkage and distortion being minimal.

The serial sections were mounted on slides coated with 2% gelatine, exposed briefly to formol vapour to form irreversible gel. The sections were cleaned by washing in ascending grades of alcohol and Xylol and then through descending grades of alcohol. They were stained for 15 minutes in Toludine-blue ("Michrome" Edward Gurr), after dehydration in alcohol, they were differentiated in Golthard's differentiator and finally cleared in absolute alcohol, alcohol and Xylol and finally mounted in D.P.X. mount (B.D.H.).

EXPERIMENTAL RESULTS

VISUAL PROJECTION MAP ON THE SURFACE OF THE DORSAL NUCLEUS OF THE LATERAL GENICULATE BODY

Eight rabbits were investigated in mapping the projection of the left visual field on the dorsal nucleus of the right lateral geniculate body and a total of 173 electrode penetrations were made into the nucleus in this process, at 500 microns intervals - mediolaterally as well as anteroposteriorly.

"Multi-unit" responses of shortest latency only were taken into account in localizing them on the perimeter. Having recorded from the surface of the dorsal nucleus of the lateral geniculate body, individual electrode penetration was continued downwards into the nucleus, stopping at every 400 micron intervals and localizing the visual response on the perimeter therefrom, till cessation of visual response.

Experiment RLGB6, in which 23 out of 30 electrode penetrations were histologically confirmed to be within the dorsal nucleus of the lateral geniculate body was utilised in constructing projection maps of the visual field, on the surface as well as in depth.

The first localized response, encountered at the depth of about 6.5 mm. from the cortical

surface, of all the electrodes provided the projection map on the surface of the nucleus, an area 2.5 to 3 mm. sq. For elucidation of projection of visual field in the depth of the nucleus, a series of maps were constructed in the following way. Visual responses at 400 microns intervals, in depth, were plotted for all the electrode penetrations in a single medio-lateral row. This represented the field projection within the nucleus at a particular coronal plane. Next row of medio-laterally placed electrodes were utilized for the projection map construction at the next coronal plane which was 500 microns away from the previous one, and so on. Next a model of visual projection in depth of the dorsal nucleus of the lateral geniculate body was made by planting a series of long needles at calculated intervals representing individual electrode penetrations, and thin plasticine sheets of different colour representing the principal meridians - 0° - 0°, 0° - 180°, 0° - 90° and 0° - 270° - were inserted in between and through the needles, as observed in the maps of various coronal planes of nucleus. This revealed the manner in which the meridians extended into the depth of the nucleus.

1. VISUAL FIELD PROJECTION ON THE SURFACE OF THE DORSAL NUCLEUS.

In analysis of the projection of the visual field on the surface of the dorsal nucleus of the lateral geniculate body, the characteristics of the whole field, as recorded on the perimeter is considered first. Figure 3a shows the perimetric localization of the surface responses in the experiment RLGB6. The whole field is a naso-temporal band. The peripheral extension of the band is more in the nasal field than in the temporal. With the successive penetration of the electrode from the lateral to the medial side, on the surface of the nucleus, the visual response shifts from the temporal to the nasal field, and with that from the anterior to the posterior on the surface the response shifts from the upper to the lower field. Though the majority of the electrode penetrations were 500 microns apart, antero-posteriorly as well as medio-laterally, the response shifts in bigger steps, in the field, in medio-lateral movement of the electrode than the antero-posterior. This band-shaped arrangement of the whole of the responding field is confirmed in experiment RLGB2 (Fig. 4a), in which 13 out of 24 electrode penetrations were histologically confirmed to be within the dorsal nucleus of the

lateral geniculate body, and also in experiment RLGB9, in which 15 out of 21 electrodes penetrations were confirmed histologically to be within the dorsal nucleus. The visual responses from the electrode penetrations through the brachium of the superior colliculus were not taken into account in the projection map construction of the dorsal nucleus of the lateral geniculate body.

Responses from a group of postero-medially placed electrodes (on the surface) were encountered, that did not follow the trend of the responses shifting nasally as the electrode moved medially on the surface of the nucleus. On the contrary, their localization was further temporal than those from the immediate lateral electrode penetrations. In figure 3a such points of response-localization are indicated by filled circles, joined with interrupted lines with those from the other electrode penetrations of the same row. That these nonconforming responses were consistently obtained from the postero-medial segment of the surface, was confirmed in experiment RLGB9.

The projection map of the visual field on the surface of the dorsal nucleus of the lateral geniculate body, of experiment RLGB6, is shown in figure 3b. In this experiment the middle

and the posterior parts of the dorsal nucleus were explored. The nasal half of the visual field is projected on the medial side of the surface, the temporal half laterally, the upper field anteriorly and the lower field posteriorly. All the sectors of the visual field are not symmetrically projected. The nasal visual field between the meridians 150° - 240° occupies the major part of the surface. Of the remaining surface a considerable area is devoted to the visual field between the meridians 60° - 330°; as a consequence the visual fields between the meridians 150° to 60° and 330° to 240° are compressed to mere stripes in their projection on the surface. The circles of equiangular deviations from the centre of the perimeter, at 10° intervals, are distorted into ellipses with their major axes approximately along the vertical meridian 90° - 270°. Along the horizontal 0° - 180° meridian these distorted circles of equiangular deviations are more closely packed near the centre, up to 50° to 60°. Beyond this a significant spreading out is observed in these distorted circles, up to 80°, in the peripheral nasal field. This nasal peripheral spread-out of the circles of equiangular deviation well coincides with that of the meridians between 150° - 240°, indicating

a higher magnification of this part of the visual field. Along the vertical 90° - 270° meridian, the situation is reverse; these circles are closely packed in the periphery and fairly spread-out near the centre (fig. 3b, 4b).

The object of the aforementioned distortions are presumed to facilitate a magnified projection, across the surface of the dorsal nucleus, of the band of concentrated retinal ganglion cells - the visual streak - which lies below and parallel to the lower margin of the myelinated nerve fibres. The indirect-ophthalmoscopic observation of obliquity in the position of the myelinated nerve fibres, hence the visual streak, explains the oblique extension of the whole of the visual field from the upper temporal to the lower nasal field.(3a)

Some disparity, regarding the total nucleus surface area devoted to individual sectors of the visual field, was noticed in different experimental result analysis. For example the point of intersection of the meridians is more medially projected in experiment RLGB9 than in experiment RLGB6, and as a consequence observation of more of the temporal field on the surface in the latter experiment could be attributed to the unavoidable variation in aligning the rabbits eye to the centre of the

perimeter. Furthermore, in experiment RLGB9 intercrossing of the lines joining the responses of electrode penetrations of a single medio-lateral row is observed which is ascribed to some amount of eye movement (as the eye was not fixed by a limbal-ring in these experiments) during the experiment. However all the experiments are in agreement about the band-shaped extension of the visual field and its nasal, temporal, upper and lower projections being on the medial, lateral, anterior and posterior parts of the surface respectively.

The postero-medial segment of the surface is segregated in figure 3b by a diagonal line, as responses from this area do not conform with the projection map of the rest of the surface. With the available data, it is not possible to construct a secondary projection map showing mirror-imaging of the whole principal map. However, a reduplication of the adjacent visual field is comprehensible in both experiment RLGB6 and 9.

2. PROJECTION OF THE VISUAL FIELD IN THE DEPTH OF THE DORSAL NUCLEUS OF THE LATERAL GENICULATE BODY

A series of visual-field-projection maps were constructed, at coronal planes 500 microns

apart from experiment RLGB6 (fig. 6, 7, 8 and 9).

The different meridians of the visual field are observed to extend into the substance of the dorsal nucleus as corresponding planes. These planes do not pursue a straight vertical course; instead they deviate considerably from their points of origin on the surface of the nucleus. The nasal horizontal meridian 0^{o} - 180^{o}, which lies on the surface, between the two most anterior rows of electrode penetrations (fig.3b), is observed to lie between the two most dorsal rows of responses, in the coronal-map 500 microns anterior to the surface position of it; at this plane it loses its surface representation. This indicates that plane 0^{o} - 180^{o} shifts anteriorly as it moves ventralwards (fig. 6b). The planes 0^{o} - 0^{o} and 0^{o} - 270^{o} which are observed to radiate postero-laterally, on the surface, have an oblique course directing ventro-medially in their course into the nucleus substance. Anteriorly, where these meridians lose their surface representation, are represented in the depth of the nucleus. In course of their downward descent the distance between them decreases gradually, indicating progressive fall in the magnification of the field between them. Posteriorly, where they have both surface and depth representation, these two planes deviate

considerably towards the lateral surface of the nucleus as well as approach each other, thereby increasing the representation between 180° - 270° medially and 0° - 90° laterally. A negligible representation for plane 0° - 90° was observed. The reason for meridians' change in course, in their ventral invasion is presumably (a) further representation of the peripheral temporal field in depth on the lateral side of the nucleus as evident by the fact that on the surface only up to 30° - 50° is being represented (fig. 3b) whereas representation extends to 80° - 90° of the circles of equiangular deviation in depth (fig. 6b and 7b); (b) accommodation of the binocular field projection, without having to minimize the representation of the contralateral nasal field. The lower nasal field, in addition to its considerable surface representation enjoys a generous representation in depth. The most medial part of this depth projection of the contralateral nasal, lower peripheral field, also receives ipsilateral projection. The lower field, which is so ill represented, compared with the upper (fig. 3b and 5b), is well represented in depth (fig. 6b).

The vertical distance through which visual response was elicited from individual electrode

penetrations was compared with the dorsoventral measurements of the nucleus, in histological sections bearing the corresponding tracks.

3. PROJECTION OF THE BINOCULAR VISUAL FIELD ON THE DORSAL NUCLEUS OF THE LATERAL GENICULATE BODY

Four rabbits (RLGB 4, 10, 11 and 12) were investigated for the determination of the projection of the binocular visual field on the dorsal nucleus of the lateral geniculate body. The area subserving binocular vision is observed to be located in the depth of the dorsal nucleus 200 to 300 microns below the surface. It is medially placed and is 1.5 to 1.6 mm. posterior to the anterior margin of the nucleus. Its vertical extent varied from 500 to 800 microns and the anteroposterior extent between 500 - 600 microns. The mediolateral extent was 500 microns approximately (fig. 10).

4. SINGLE UNIT ACTIVITY OF THE DORSAL NUCLEUS OF THE LATERAL GENICULATE BODY

In course of this study the activity of only 18 single units have so far been observed. The rabbits investigated had no correction for error of refraction and no aid for near vision. Such paucity of observation does not lead to any logical conclusion regarding the physiological

organization of the dorsal nucleus cells. However, the following analysis of individual units might help in formulation of a plausible hypothesis.

Localization of the unit in the visual field	Characteristic of the unit
(1) 18^{o} - 46^{o}	Circular receptive field, 2^{o} in diameter, with "on" response at the centre and "off" response at the periphery.
(2) 37^{o} - 40^{o}	Circular receptive field, 2^{o} in diameter, pure "on" in response without "off" surround
(3) 33^{o} - 55^{o}	Circular receptive field 2^{o} in diameter pure "on" in response without "off" surround
(4) 22^{o} - 40^{o}	Circular receptive field, 2^{o} in diameter, pure "on" in response without "off" surround
(5) 37^{o} - 30^{o}	Circular receptive field, 2^{o} in diameter, excited by "on" and "off" of the light spot without surround effect, sensitive to movement, no directional preference detected
(6) 63^{o} - 205^{o}	Circular receptive field, 2^{o} in diameter, excited by "on" and "off" of light spot without surround effect, sensitive to movement, no directional preference detected.

Localization of the unit in the visual field	Characteristic of the unit
(7) 63° - 200°	Circular receptive field, 2° in diameter, pure "off" response, without "on" surround.
(8) 63° - 202°	Circular receptive field, 2° in diameter, pure "off" in response without "on" surround.
(9) 45° - 217°	Circular receptive field, 1° in diameter, excited by "on" and "off" of light spot, no surround effect, sensitive to movement, no directional preference.
(10) 35° - 217°	Circular receptive field, 1° in diameter, excited by "on" and "off" of light spot, no surround effect, sensitive to movement, no directional preference detected.
(11) 24° - 164°	Oval field, 6° along the major axis, excited by "on" and "off" of light spot without surround effect, sensitive to movement, no directional preference detected.
(12) 4° - 246° to 90° - 52°	Approximately 90° long band, 10° wide, pure "off" in response, no "on" surround or flank, responds to movement only along the major axis of the unit.

Localization of the unit in the visual field	Characteristic of the unit
(13) 40^{o} - 50^{o}	Transversely oval receptive field, 6^{o} long 3^{o} wide, pure "off" in response without "on" surround, responds to movements, no directional preference detected.
(14) 89^{o} - 70^{o} to 68^{o} - 70^{o}	Circular receptive field 20^{o} in diameter excited by "on" and "off" of light spot, sensitive to movement, no directional preference.
(15) 84^{o} - 90^{o} to 27^{o} - 90^{o}	Band shaped receptive field, 20^{o} wide, pure "on" in response, no "off" flank or surround, movement sensitive, no directional preference.
(16) 60^{o} - 142^{o} to 25^{o} - 142^{o}	Band shaped receptive field 17^{o} wide, pure "on" in response, no "off" surround or flank, not sensitive to movement.
(17) 40^{o} - 180^{o}	Circular receptive field, pure "on" in response, 2^{o} in diameter, no "off" surround.
(18) 82^{o} - 175^{o}	Circular receptive field, 3^{o} diameter, pure "on" in response, no surround, sensitive to movement, no directional preference.

These units were recorded from the surface as well as the depths of the dorsal nucleus of the lateral geniculate body and were checked histologically by lesions made at known depth.

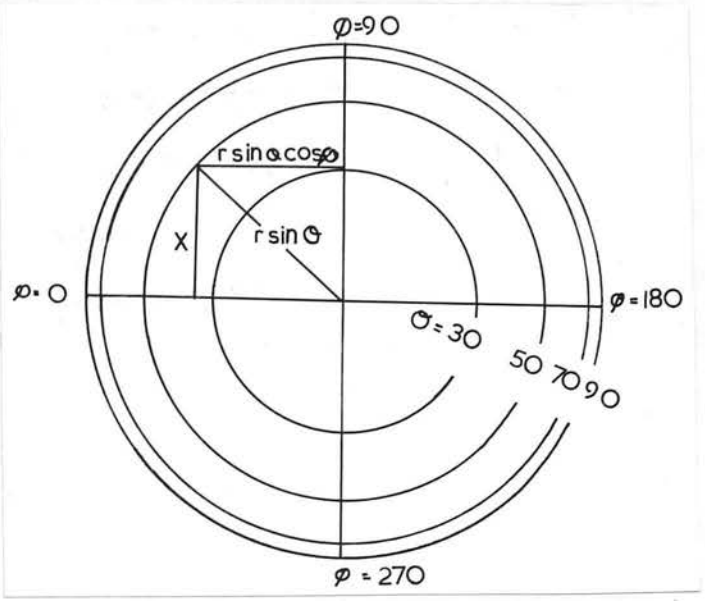
It is observed that the units with small receptive fields are located in that part of the nucleus where the visual streak is projected, much more magnified than the rest of the field. The units with larger fields are located in nuclear areas devoted to the projection of the visual field outside that of the streak.

5. VISUAL PROJECTION MAP ON THE CORTEX

Twelve rabbits were investigated in mapping the projection of the left visual field on the right hemisphere of the cortex.

In experiment RCTX10, 68 electrode penetrations were made of which 49 yielded visual responses, which helped in construction of the cortical projection map.

For a comprehensible comparison with the existing visual-cortical projection map of the rabbit (Thompson, Woolsey and Talbot 1953), the experimental data of the present study, obtained in spherical-polar co-ordinates with axis through the reference point, were transferred to parallel co-ordinates.



In a perimeter the stimulating light is positioned on the surface of a sphere with the eye at its centre. A line drawn from the perimetric pole through the centre of the eye is defined as the reference axis. Under experimental conditions the reference axis is arranged horizontally, and the horizontal plane passing through the reference axis is the plane of reference. The position of the stimulating light is determined by two angles: the angular distance (θ) from the reference axis and the angle with a perpendicular from the light to the reference axis makes with the reference plane (φ). To plot points of this spherical surface on a plane, projection is made from the sphere to a cylinder with its axis along the $= 90^{\circ} - 270^{\circ}$ line, i.e. the vertical line through the centre of the eye. In the plane representation the distance X of the stimulating light from the reference plane is plotted against the angle Y between a perpendicular from the light to the

cylinder axis and the vertical plane through the reference axis. For a given position of the light ($\theta\varphi$), the distance of the light from the reference axis is r sin θ , where r is the radius of the sphere. Its distance from the reference plane x = r sin θ sin φ

The angle Y is given by the equation

$$\tan Y = \frac{\sin \theta \cos \varphi}{\cos \theta}$$

A projection of the spherical surface was made first onto a plane, perpendicular to the reference axis, by drawing circles of r sin θ $\theta = 10^{\circ}, 20^{\circ}, \ldots. 80^{\circ}$. A point $\theta\varphi$ on the spherical surface was plotted in this projection from the centre along a radius at angle φ from φ = 0 line. The distance X was determined directly in millimetres. The distance r sin θ cos φ was also measured in millimetres. This figure was divided by r cos θ (i.e. 90 cos φ, since r = 90 mm.) to give Y. Y was then found from the tangent table and X plotted against Y.

In dorsal approach of the cortex, it was observed that area subserving vision had an antero-posterior extension of 10.5 mm., and a medio-lateral extension of 9.5 mm. Its medial margin is 4 mm. lateral to the midline and the anterior margin 4.5 mm. posterior to the bregma.

In the cortical projection map the vertical

meridian "O - V" which is approximately parallel with the midline, divides the visual area unequally into a major lateral part and a minor medial part, the nasal visual field being represented on the lateral half of the cortex and the temporal medially. In their cortical projection the vertical meridians of the nasal field are placed in close proximity of the principal meridian "O - V" up N40° throughout their extent. Whereas the meridians beyond N40° representing the peripheral nasal field are spread out unevenly, more spreading occurring on the postero-lateral aspect of the visual cortex than antero-laterally. The vertical meridians of the temporal field are in general closely packed in their cortical projection and only meridian T20° tranversing the whole antero-posterior length of the visual cortex, the other two meridians T40 and T60, are represented about half way down the visual cortex.

The horizontal meridian "O - H" divides the cortex transversely into a major anterior half and negligible posterior half of which lower part of the visual field projected anteriorly and the upper part posteriorly. The projection of the field between "O - H" and -20° of the visual field is more magnified than the rest The projection of the "visual-streak" itself is

not uniform throughout its whole extent, the nasal field, projected on the lateral half of the cortex, being more magnified than temporal field, projected on the temporal half of the cortex. The spreading up of the horizontal meridians postero-laterally coincides well with that of the peripheral vertical meridians indicating a significant magnification of the nasal field, along the projection of the visual-streak (fig. 13).

The responses from the extreme antero-lateral sector of the visual cortex do not conform with the principal projection map. The lateral boundary of this area lies about 600 microns down the lateral surface of the visual cortex which was approached by the most laterally penetrated electrodes driven vertically downwards at 200 microns steps.

Three rabbits were investigated under nembutal (pendobarbital-sodium) anaesthesia, following the dose recommended by Thompson et al (1950). The cortex was approached from the lateral side following a wide lateral exposure (fig. 1(b)). In this series cortical visual responses were obtained in one experiment only. In this experiment four medio-lateral rows of 38 electrode penetrations were made, starting 5.5 mm. posterior to bregma. The

pattern of the visual field projection observed in this experiment was in conformity with that observed under urethane anaesthesia and dorsal approach of the cortex. As in experiment RCTX10, responses from the nasal visual field were recorded from the lateral side of the cortex and those from the temporal visual field, from the medial side. The responses from the most lateral electrode penetrations of the anterior two rows showed reduplication of the nasal field of the primary area. This was in conformity with experiment RCTX10, where reduplication of the nasal field was observed on the antero-lateral visual cortex.

In this experiment, the medio-lateral extent of the visual area was observed to be 11 mm. instead of 9.5 mm. as observed in experiment RCTX10.

6. PROJECTION OF THE BINOCULAR VISUAL FIELD ON THE CORTEX

Two rabbits were investigated in mapping the projection of the binocular visual field on the cortex. In the binocular cortical area, localized responses were observed simultaneously from the ipsilateral and the contralateral eye. The ipsilateral responses are localized further nasal to the corresponding contralateral response. The responses from the contralateral eye served

as a guide in determining the location of the binocular projection, in relation to the primary and the secondary areas. The simultaneous ipsilateral and the contralateral responses are obtained from the anterolateral part of the primary visual cortex where the contralateral nasal peripheral field is projected. For, in a mediolateral row of electrode penetrations, as the electrode is moved from the medial to the lateral side on the cortex, the contralateral localization shifts from the central to the peripheral visual field, throughout the whole binocular area. The secondary visual area was not explored for binocular projection. Diffuse responses were obtained from the most anterior group of electrode penetrations (fig. 14).

7. REFRACTION IN RABBITS

Of the fifty-two rabbits refracted all of them were observed to be hypermetropic, majority within the range of + 4.0D sph to +4.50D sph. in both eyes. Dissimilar refraction in the two eyes was observed in three rabbits, range of disparity being +1.0D sph. to +1.50D sph. Of the four rabbits with astigmatism all had the more hypermetropic vertical meridian range of disparity between the meridians being +0.50D sph to +1.0D sph.

The object of this study has been the investigation of the cortical and subcortical projection of the rabbits' visual field, with particular emphasis on the magnification that certain regions of the visual field undergo in the process.

I THE DORSAL NUCLEUS OF THE LATERAL GENICULATE BODY

In their Marchi study of degeneration following restricted retinal lesions, Brouwer (1923) and Overbosch (1926, quoted by Brouwer and Zeeman 1926) assume that a pair of antero-posteriorly directed horizontal and vertical planes divide the dorsal nucleus of the lateral geniculate body into four unequal segments, on which the four retinal sectors are projected. The dorsal segments of the nucleus receive fibres from the lower nasal and temporal retina (the upper visual field) and the medial segments from the upper and lower temporal retina (the nasal visual fields). The ipsilateral temporal fibres are projected medially in the depth of the nucleus, upper fibres ventrally and the lower fibres dorsally. Brouwer and Overbosch arbitrarily divide the retina into four quadrants, disregarding the structure and orientation of the "visual streak". Such

quadrantic subdivision of the retina, though of advantage in animals with concentrically arranged retinal ganglion cells, with maximum density at its centre, is ill-suited in the rabbit, because of the linear disposition of the retinal ganglion cells along the "visual streak".

In the present study a congruence is observed to exist between the concentration and orientation of the retinal ganglion cells and the visual field projection on the higher centres. Most of the rabbit's band-shaped visual field is projected, unequally magnified, on the surface of the dorsal nucleus of the lateral geniculate body, contrary to Brouwer and Overbosch's findings, which preclude the possibility of the projection of the whole visual field on the surface of the nucleus. The projection of the "visual streak", which gains maximum magnification, is orientated medio-laterally on the surface of the nucleus, with the nasal visual field directed medially. The medial projection of the nasal field is, however, in agreement with observation of Brouwer and Overbosch that the temporal retinal fibres are projected medially on the nucleus. The fields above and below the "visual streak" are projected anterior and posterior to that of the "visual streak" itself. The projection of the field outside

the "visual streak" is much less magnified than that of the "visual streak". The magnification is not uniform all along the projection of the "visual streak". A gradual increase in magnification is observed from the temporal to the nasal field. From the surface the projection of the "visual streak" extends ventrally in the depth of the nucleus with an increase in the magnification of the projection of the whole streak in general and that of the area responsible for the nasal visual field in particular. The observation that the monocular visual field projected, on the surface of the nucleus, as a horizontal band of limited width is in agreement with that of Seneviratne (1963) and Kerr and Seneviratne (1963) in the rabbit's superior colliculus. Seneviratne's observed that, in the superior colliculus, "there is probably, in the vicinity of the true fixation axis, a small retinal area where in the resolution seems minimally enhanced; ... there may be in the temporal retina a corresponding retinal area of slightly increased resolution anterior nasal vision." This also holds good in the case of the dorsal nucleus of the lateral geniculate body. In the depth of the nucleus, in addition to the visual field projected on the surface, more of the lower visual field is represented.

The localization of responses, from the neighbourhood of a particular point in the visual field on the surface of the nucleus, as well as several times in its depth indicates, a priori, that retinal ganglion cells, corresponding to a particular point of localization in the visual field, is projected on to a dorso-ventrally orientated column of cells in the nucleus. This columnar projection is not likely to be a straight line, as the principal meridians of the depth maps of the nucleus, in this study, show a curved course within the nucleus. This presumption is consistent with Le Gros Clark's (1940 - 41) anatomical observation of the "receptive unit" - which is a columnar arrangement of cells involving all the layers of the monkey's lateral geniculate body connected with the corresponding points in the two retinae. In their electro-physiological study, Bishop, Kozak, Levick and Vakkur (1962) confirm the same phenomenon in the cat's lateral geniculate body, they call it a projection line. No attempt has been made to elucidate the physiological organization of cells along a "receptive unit" in this study.

The projection of the ipsilateral visual field, as observed in this study, is in agreement with that of Brouwer and of Overbosch.

This field is projected on the medial side of the nucleus, 200 to 300 microns deep to the surface. The vertical, horizontal and antero-posterior extents of this area are 500 to 800 microns, 500 microns and 500 to 600 microns respectively. It is located 1.5 to 1.6 mm. posterior to the anterior margin of the nucleus.

The surface responses from the postero-medial aspect of the dorsal nucleus of the lateral geniculate body do not conform with its principal projection map. Though the responses from this secondary area of the nucleus do not form a strict mirror image of the primary area, a reduplication of the lower nasal visual field of the primary area is indisputable. In the dorsal nucleus of the lateral geniculate body, the existence of the secondary area is by no means unique in the rabbit. For, in the cat, a secondary area on the "medial tip of the nucleus" was observed by Seneviratne and Whitteridge (1962) and alluded to by Bishop, Kozak, Levick and Vakkur (1963).

The object of single unit observation in the present study has been the investigation of the physiological organization of the dorsal nucleus cells within and outside the projection of the "visual streak". The limited number of single units observed in this study can be

grouped under two headings - those with comparatively small receptive field and those with comparatively large receptive fields. Arden (1963a, 1963b) also observed a difference of size in the receptive fields in the lateral geniculate units in the rabbit. In his simple units with small receptive fields Arden observes an irregularity in their outline, contrary to circular fields with no apparent irregularity in their outline of the present study. Arden's irregular outline in receptive field could be attributed to his light anaesthesia and non-immobilization of the eye of the rabbit. The receptive field size up to 6^{o} is classed under the group of small units and the big units have a receptive field size up to 90^{o} long and 10^{o} to 20^{o} wide. The small receptive field units are observed to lie along the "visual streak" projection whereas those with large receptive fields lie outside it. The higher magnification of the visual streak projection is presumed to be due to these small receptive field units. A smaller shift in the visual field is likely to occur, when the recording electrode is moved, at constant intervals, through a population of cells with small receptive fields than through those with large ones.

It is further presumed that the units with small receptive fields maintain one-to-one connection with retinal ganglion cells, as their size of up to 6^{o} is in agreement with Barlow and Hill's (1963) observation of 5^{o} as the size of the retinal ganglion cell units. On the other hand a connection with multiple ganglion cells is likely to be responsible for units with large receptive field. Such multiple ganglion cell connection has been observed by Glees (1941 - 42) in the rabbits dorsal nucleus. Though Glees does not clarify the distribution of the multiple connections, it is unlikely the whole dorsal nucleus receives such multiple connection uniformly.

II THE CORTICAL SURFACE

In the present study the visually excitable area of the cortex is observed to be located in its posterior part in the rabbit. This area starts 4.0 to 4.5 mm. posterior to the bregma and extends posteriorly for 10.5 mm, approximately to the posterior pole. The medio-lateral extension of this area is 11.0 mm. with its medial margin 4 mm. lateral to the midline. The antero-posterior extension of the visual area as observed in the present study is near agreement with Bishop and O'Leary's (1936)

finding of 12 - 15 mm, observed with penetrating electrodes. The present observation is about 4.5 mm. short of Thompson, Woolsey and Talbot's (1950) finding of 15 mm. observed with a cotton thread electrode contained in a small steel tube. With a "cotton thread electrode" it is very difficult to know whether the electrode has made the amount of excursion as indicated by its manipulator. Besides, in a pulsating cortex it is not easy to retain the electrode in one position. However the medio-lateral extent is in agreement with that of Bishop et al (1936) as well as Thompson et al (1950).

As in the dorsal nucleus of the lateral geniculate body, the projection of the "visual streak" is more magnified than the rest of the field. The "visual streak" projection is orientated approximately medio-laterally on the cortex, with the area representing the nasal visual field directed lateral. The field above and below the "visual streak" is projected posterior and anterior to its cortical projection. In the upper visual field posterior to the streak-projection, that from the upper-nasal part is lacking. This is attributed to the fact that the vertically driven electrodes do not reach the steep lateral side of the

posterior part of the cortex. The pattern of visual field projection is in disagreement with the observation of Putnam and Putnam (1926) who state that inferior retinal (the upper visual field) is projected on the lateral side of the cortex and the temporal retinal (the nasal visual field) anteriorly. In the observation of Thompson et al, the upper field is stated to be projected postero-laterally, in the primary area, the lower field antero-medially, the nasal field antero-laterally and the temporal field postero-medially. This is in near agreement with the observations of the present study, where the upper field is projected more posteriorly and the nasal field more laterally. However, these are minor differences, and could be ascribed to biological variation. The point of major disagreement is the extensive representation of the nasal field in general and the nasal part of "visual streak" projection in particular. Though Thompson et al observe the nasal field projection to be 10^{o} more than that of the temporal field but in their observation the cortical area devoted to nasal and temporal fields are approximately equal which allows the nasal field to be less magnified than the temporal. Besides they do not comment on the higher magnification along the "visual streak" projection.

The magnification of the "visual streak" projection deserves especial attention. From Seneviratne's (1963) observation of uniform concentration of the retinal ganglion cells along the streak, the legitimate expectation would be a higher but symmetrically magnified projection of the "visual streak". But it is not so; along its projection, the magnification of the nasal field is much higher than the temporal. In monkeys, Woolsey, Marshall and Bard (1942) suggest that - "The "functional" value of different skin fields is reflected at the cortical level by the larger amount of tissue devoted to the skin areas possessing greatest tactile acuity (innervation density)". This hypothesis seems to hold good in the cortex of the monkey and the cat, (Talbot and Marshall 1941, Daniel and Whitteridge 1961), where a higher magnification for the foveal region has been observed, also Bishop et al (1963) hint that a higher magnification for the fovea exist in the cat's lateral geniculate body. The observed deviation in the rabbit's visual centres arouses the suspicion that the ganglion cell concentration of a retinal area may not be the only determining factor of its central magnification. It is suggested that, among other things, the number of retinal ganglion

cells connected with a single cell at the higher centre could also be a contributory factor.

The antero-lateral location of the secondary area, as observed in the present study, is in agreement with that of Thompson et al. However contrary to their observation of a mirror image of the whole primary area, only a reduplication of the lower nasal field of the primary area has been observed. This is congruent with the rabbit's secondary visual area in the dorsal nucleus of the lateral geniculate body.

The binocular cortical area is observed to be located in the antero-lateral part of the cortex, where the peripheral part of the contra-lateral nasal field is projected in the primary visual area. It does not seem to cover the whole of the medio-lateral extent of the visual area as suggested by Thompson et al. The observation of Thompson et al implies that ipsilateral responses extend to the upper nasal visual field, but in the present observation ipsilateral responses are obtained only from the lower nasal visual field. However observation of more nasal visual field localization of the ipsilateral responses than the corresponding simultaneous contra-lateral response supports the view of Thompson et al that during convergence of the eyes binocular vision is achieved by

superimposition of the ipsilateral over the contra-lateral nasal field.

It is adduced, from the observed magnified projection of the "visual streak", that within its visual field, which is concerned more with the lower and intermediate parts than the upper, the rabbit enjoys a band of field with better vision. The concentration of the ganglion cells in a particular retinal area, though is likely to be related to the degree of visual acuity for that area, is observed not to determine the size of the projection of that area on the cortical and subcortical centres of the rabbit. For the concentration of ganglion cells though uniform all along the "visual streak" produces more magnified projection of the area responsible for the nasal peripheral field of vision. The higher magnification in the nasal end of the band of field, the reduplication of the nasal field in the secondary cortical and subcortical centres, the extent of the binocular vision being restricted to a part of the nasal field indicate that the rabbit's nasal field is adequately equipped to cope with the embarrassment likely to be caused by a pair of laterally placed eyes in its survival.

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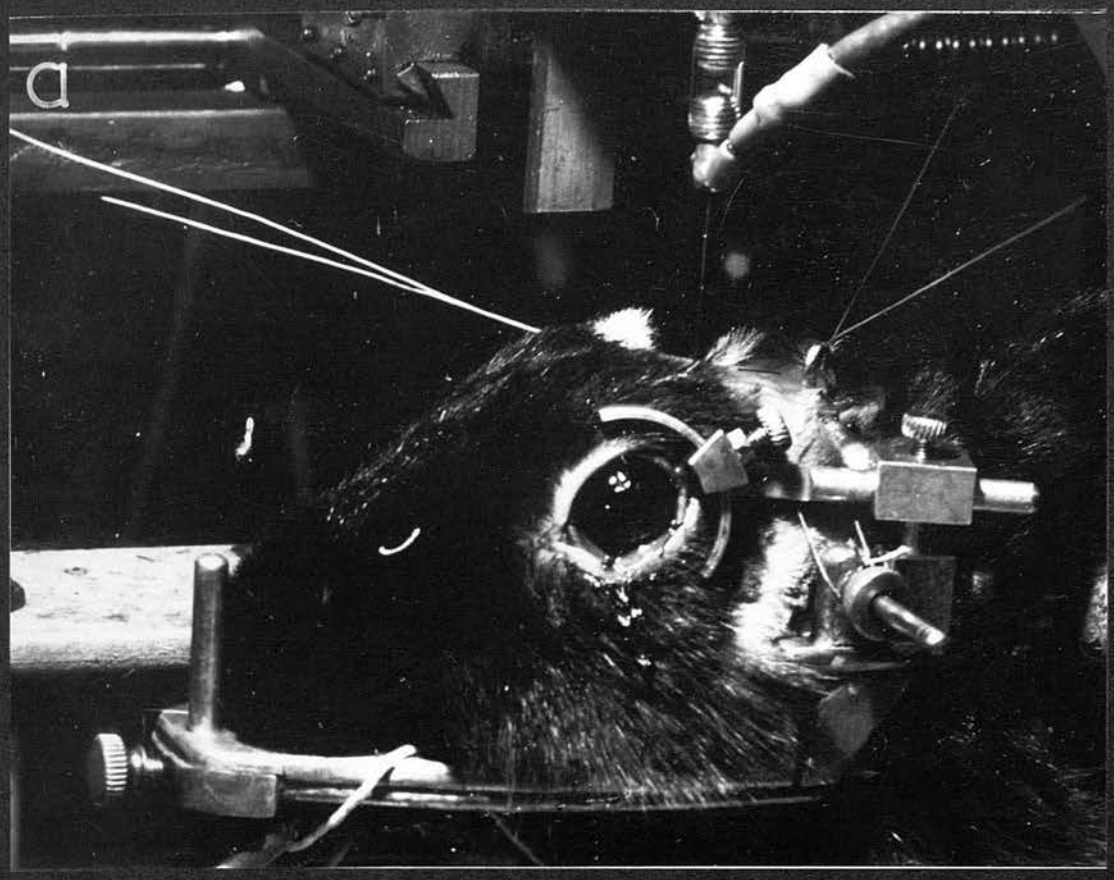
FIGURES

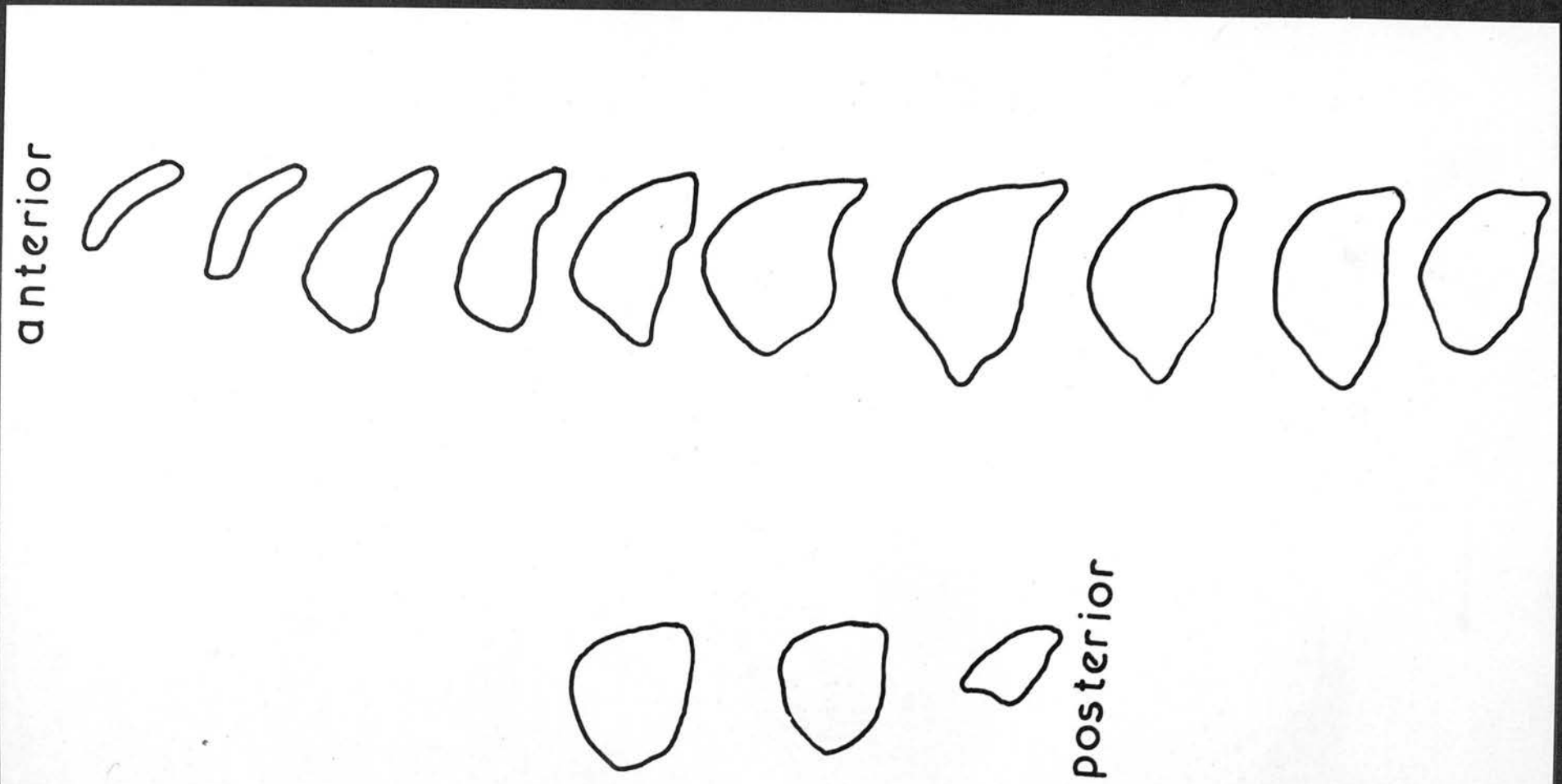
Fig. 1(a) The position of the rabbit in the steriotaxic head holder, with adjustable eye-ring, jaw-clamp, ear-plugs and electrode-bridge assembly in situ for dorsal approach of the visual cortex and the dorsal nucleus of the lateral geniculate body.

Fig. 1(b) The position of the rabbit in the steriotaxic head holder with the electrode in situ for the lateral approach of the visual cortex.


a


b

Fig. 2 Reconstruction of the right dorsal nucleus of the lateral geniculate body from coronal sections to display the shape of the nucleus.
100 micron Toludine blue sections; every second section has been represented. (magnification X10).



SERIAL CORONAL SECTIONS OF THE RIGHT DORSAL NUCLEUS OF THE LATERAL GENICULATE BODY

Fig. 3(a) Perimetric localization of visual responses from the surface of the dorsal nucleus of the lateral geniculate body. All the perimetrically localized points within the primary visual area are indicated by empty circles and those of a single medio-lateral row are joined by continuous lines. Those perimetric points in the secondary area are indicated by filled circles and are joined, with the other primary-area points in its row, by interrupted lines (spherical polar co-ordinate in RLGB6)

Fig. 3(b) Projection map of the visual field on the surface of the dorsal nucleus of the lateral geniculate body. The experimental data are sited on tracing paper covering the illustration. (Spherical polar co-ordinate in RLGB6)

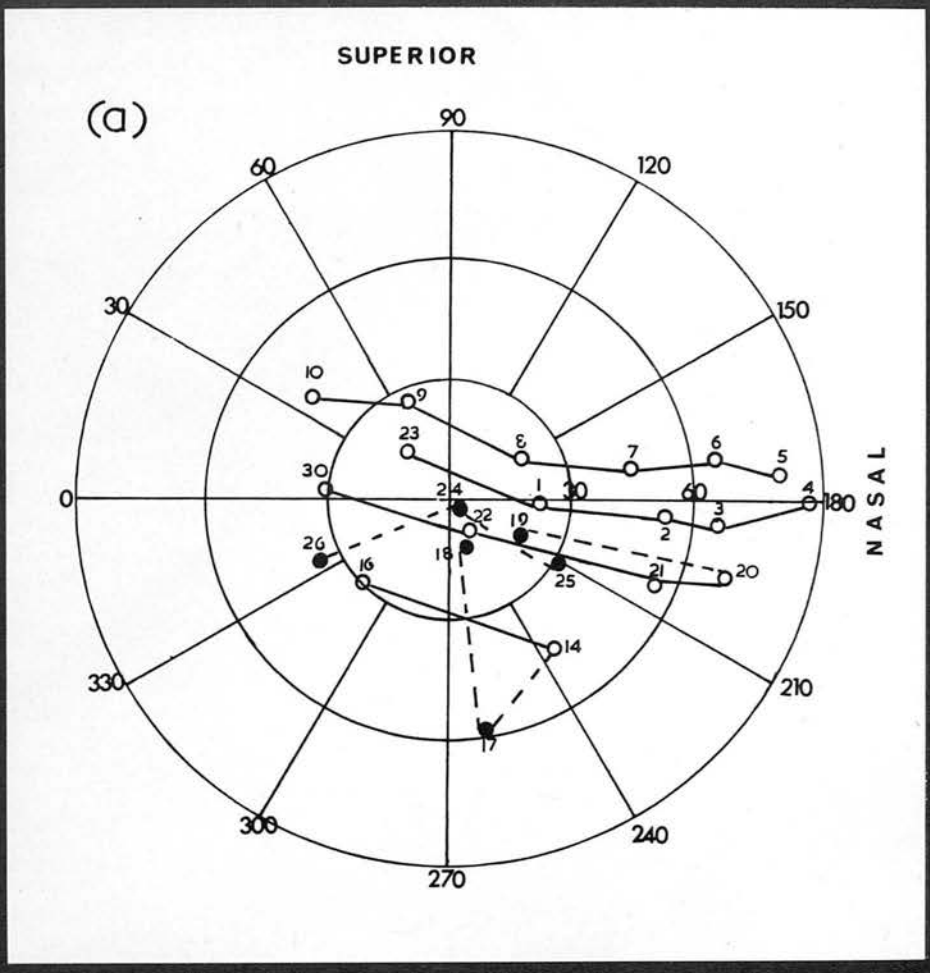

SUPERIOR
(a)
90
60
120
30
150
0
180
NASAL
330
210
300
240
270
30
60
90
120
150
180
210
240
270
300
330
0
30
60
20
40
60
80
1/2 mm
LATERAL
MEDIAL
(b)
POSTERIOR
ANTERIOR

Fig. 4 Projection map of the visual field on the surface of the dorsal nucleus (parallel co-ordinates in RLGB6).

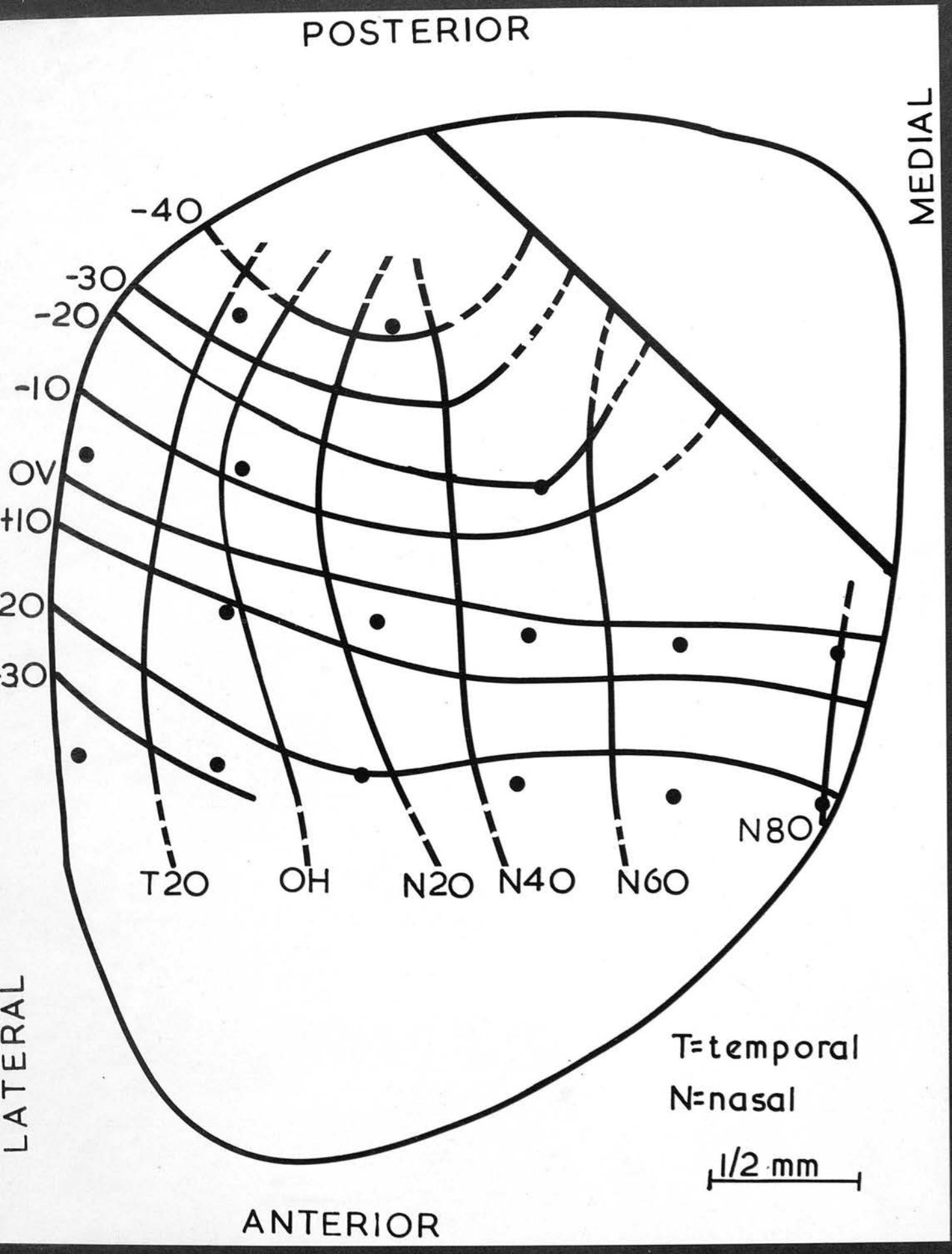
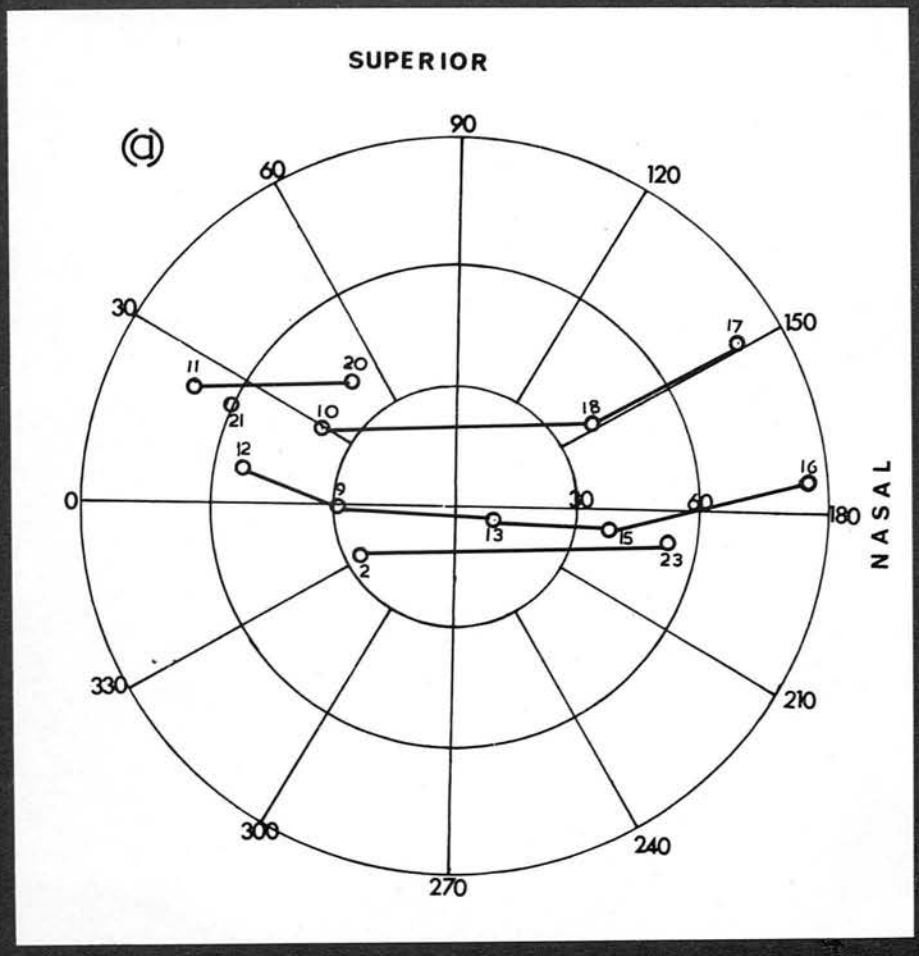

POSTERIOR
MEDIAL
-40
-30
-20
-10
OV
+10
20
30
T20
OH
N20
N40
N60
N80
LATERAL
T=temporal
N=nasal
1/2 mm
ANTERIOR

Fig. 5(a) Perimetric localization of visual responses from the surface of the dorsal nucleus of the lateral geniculate body in experiment RLGB2.

Fig. 5(b) Projection map of the visual field on the surface of the dorsal nucleus (experimental data on the tracing paper)


SUPERIOR
(a)
90
60
120
30
150
0
180
NASAL
330
210
300
240
270
11
20
21
10
18
17
12
9
30
60
16
13
15
2
23

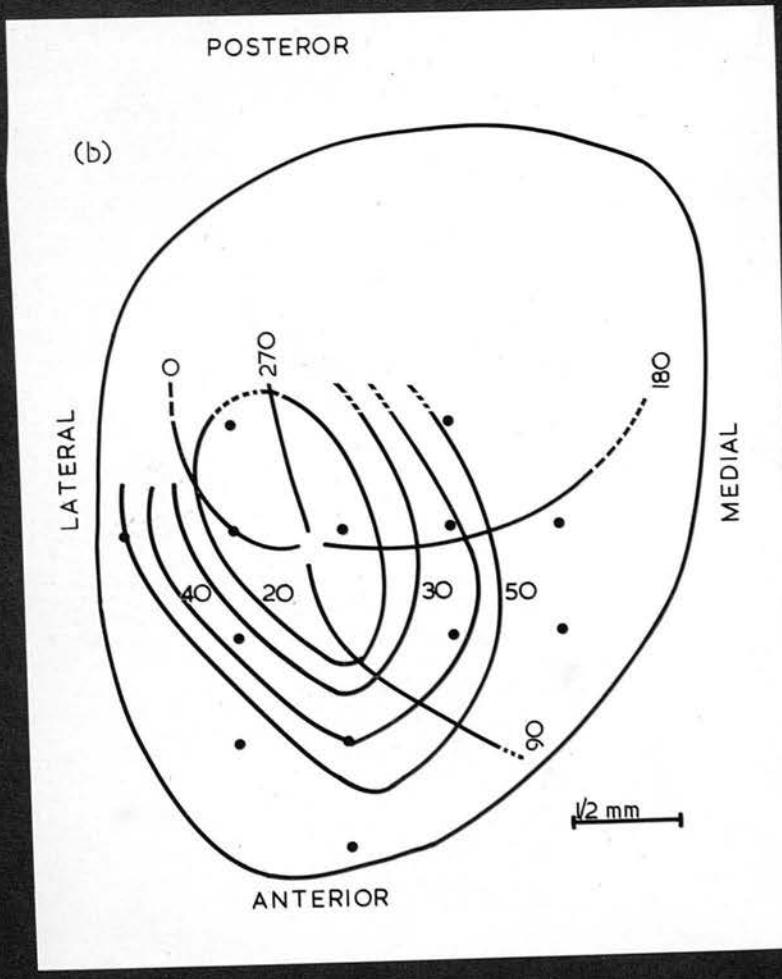
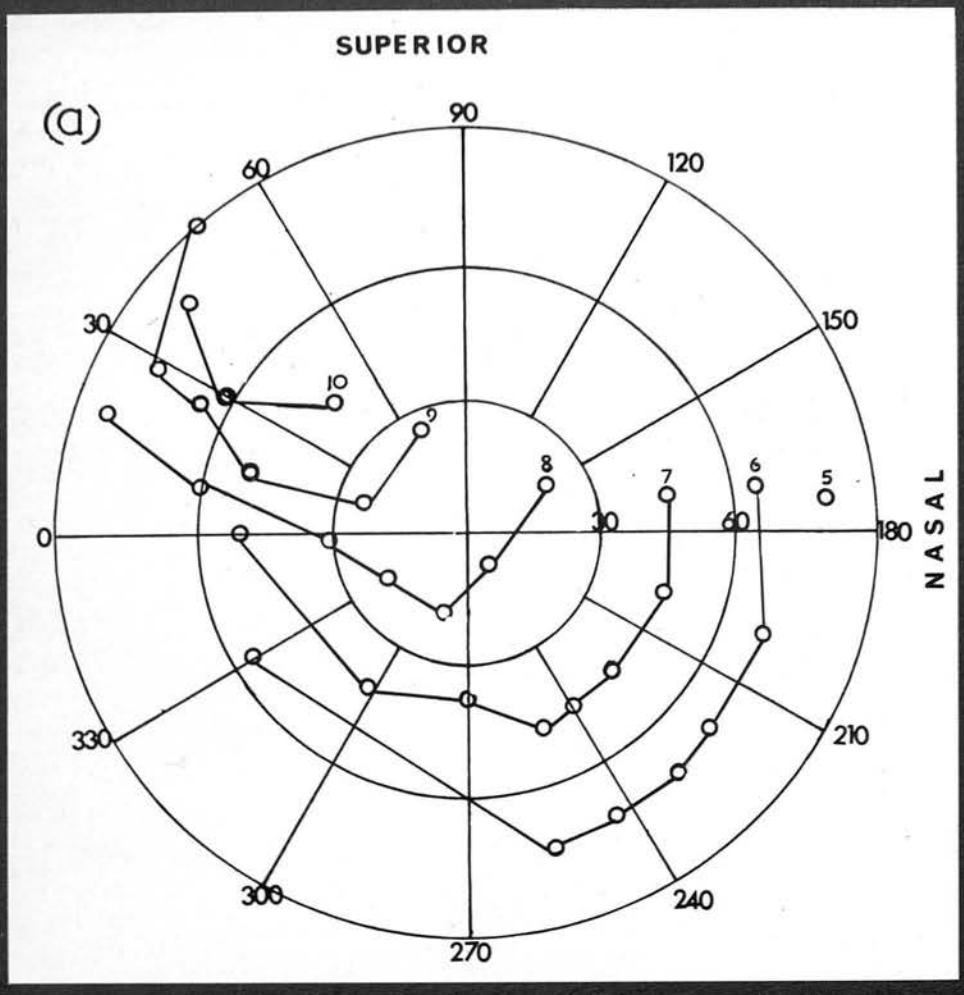

POSTEROR
(b)
LATERAL
MEDIAL
0
270
180
40
20
30
50
90
1/2 mm
ANTERIOR

Fig. 6(a) Perimetric localization of the visual responses from the depth of the dorsal nucleus of the lateral geniculate body as observed in a single medio-lateral row of electrode penetrations approximately 1 mm. posterior to the anterior margin of the nucleus. RLGB6

Fig. 6(b) Projection map of the visual field in the depth at the above mentioned coronal level, RLGB6. (experimental data on the tracing paper)


SUPERIOR
(a)
90
120
60
150
30
180
0
210
330
300
240
270
NASAL
10
9
8
7
6
5
30
60

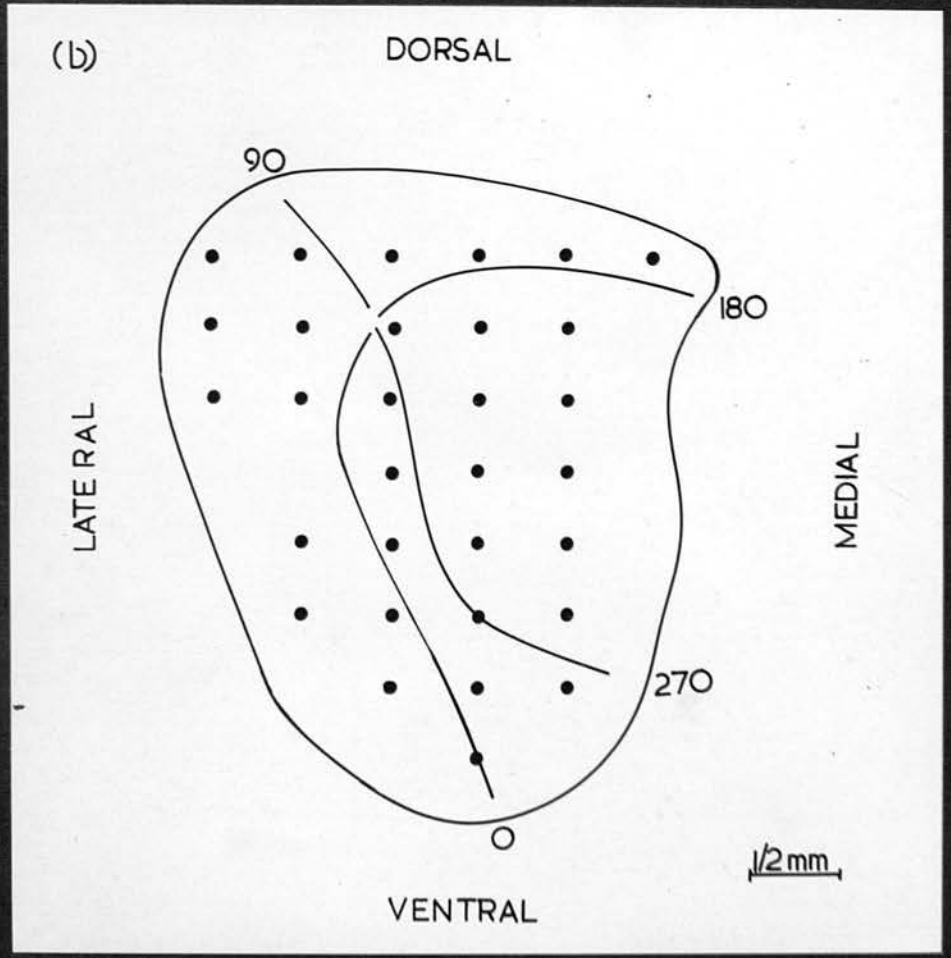
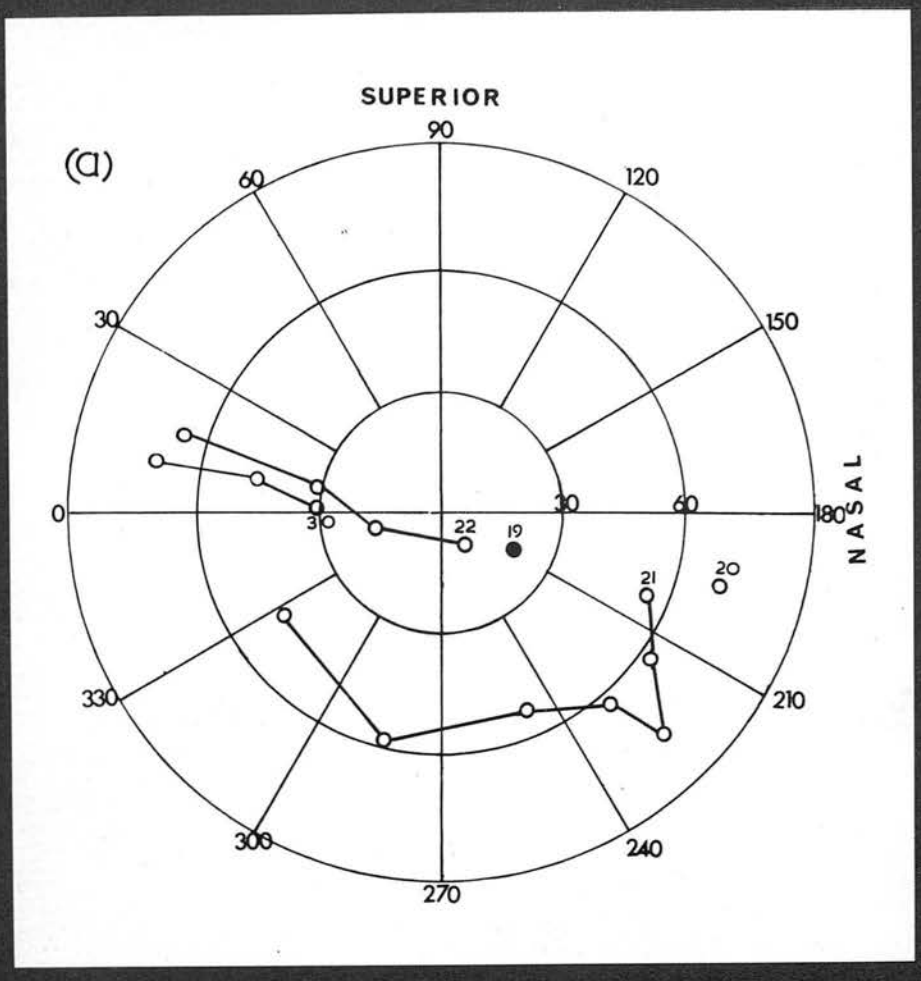

(b)
DORSAL
90
180
LATERAL
MEDIAL
270
0
1/2 mm
VENTRAL

Fig. 7(a) Perimetric localization of visual responses from the depth of the dorsal nucleus of the lateral geniculate body as observed in a single medio-lateral row of electrode penetrations 500 microns posterior to 6(a) and 6(b), in RLGB6.

Fig. 7(b) Projection map of the visual field in the depth of the dorsal nucleus at the above mentioned coronal level. (experimental data on the tracing paper).

Fig. 8(a) Perimetric localization of visual responses from the depth of the dorsal nucleus of the lateral geniculate body, as observed in a single medio-lateral row of electrode penetrations 500 microns posterior to 7(a) and 7(b), RLGB6.

Fig. 8(b) Projection map of the visual field in the depth of the dorsal nucleus at above mentioned coronal level (experimental data on the tracing paper).


(a)
SUPERIOR
90
120
60
150
30
180
0
NASAL
30
60
210
330
300
240
270
22
19
21
20

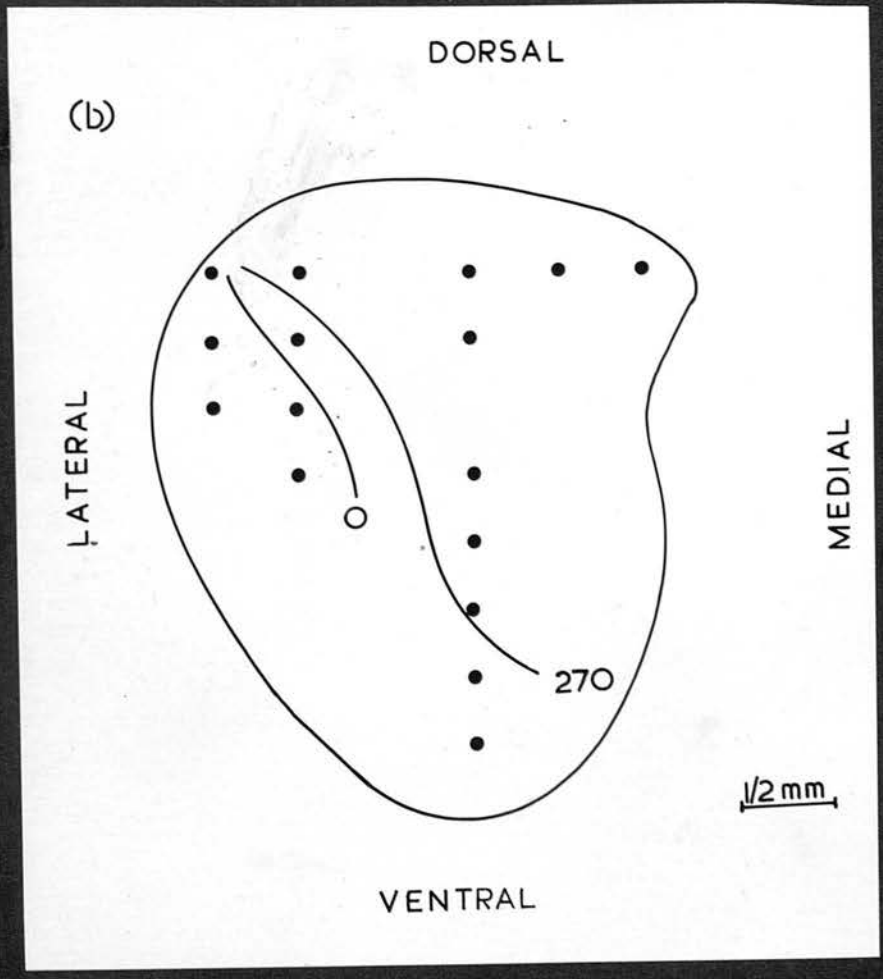
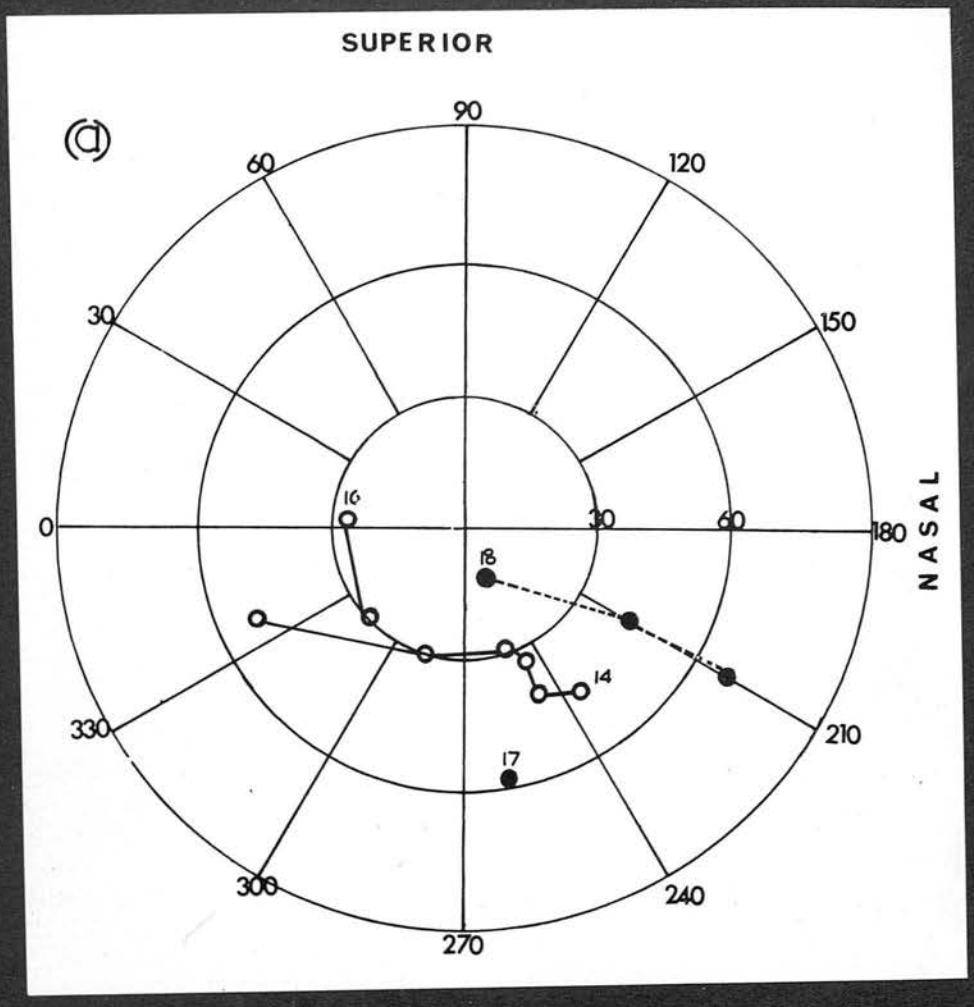

(b)
DORSAL
LATERAL
MEDIAL
270
1/2 mm
VENTRAL

Fig. 9(a) Perimetric localization of visual responses from the depth of the dorsal nucleus, posterior to 8(a) and 8(b). RLGB6.

Fig. 9(b) Projection map of the visual field in the depth of the dorsal nucleus. 1 is 500 microns posterior to 8(b) and 2 is 500 microns posterior to 1.


SUPERIOR
(a)
90
60
120
30
150
0
180
NASAL
330
210
300
240
270
16
18
14
17

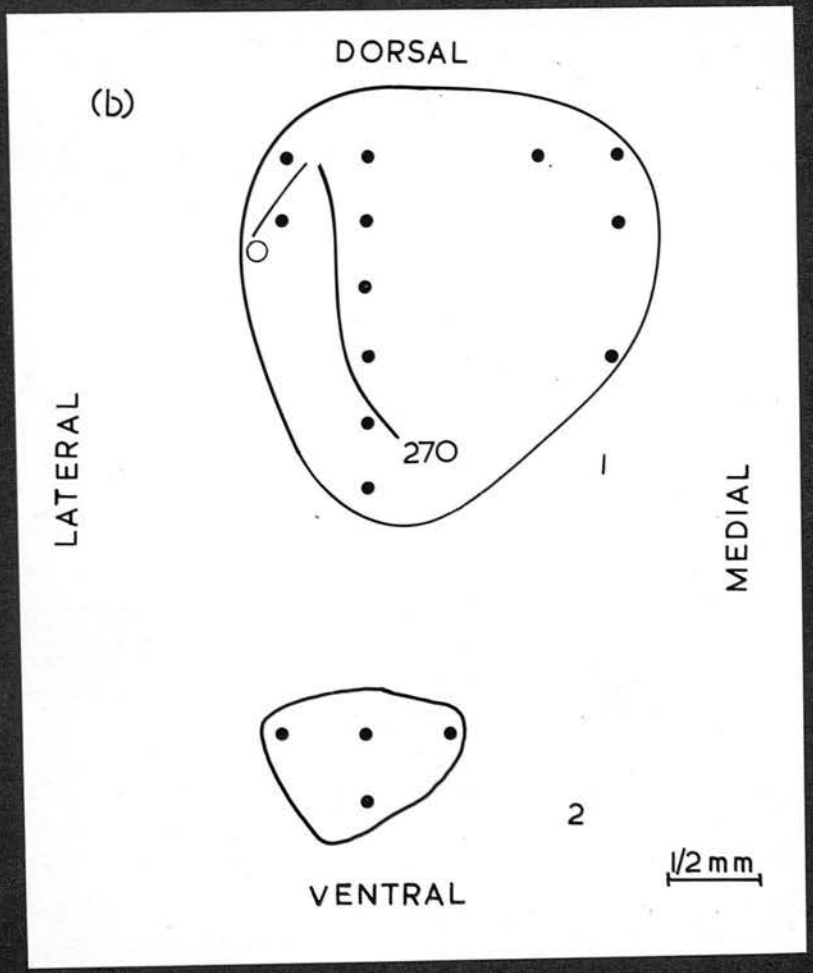
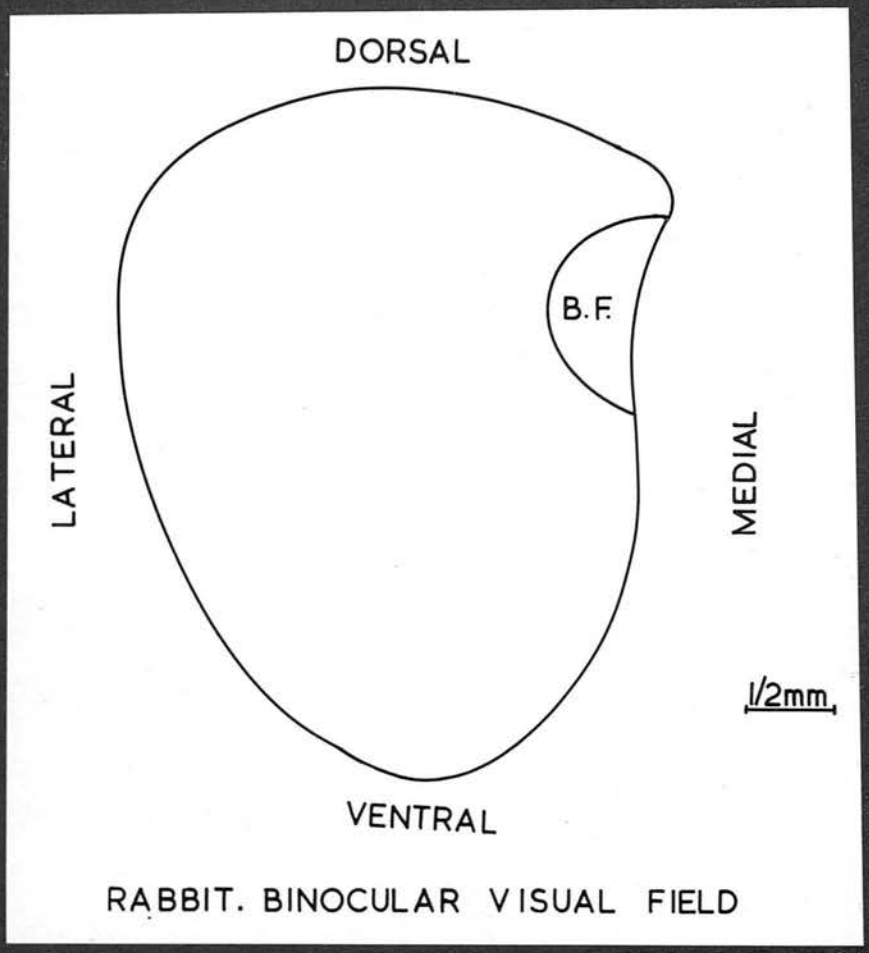
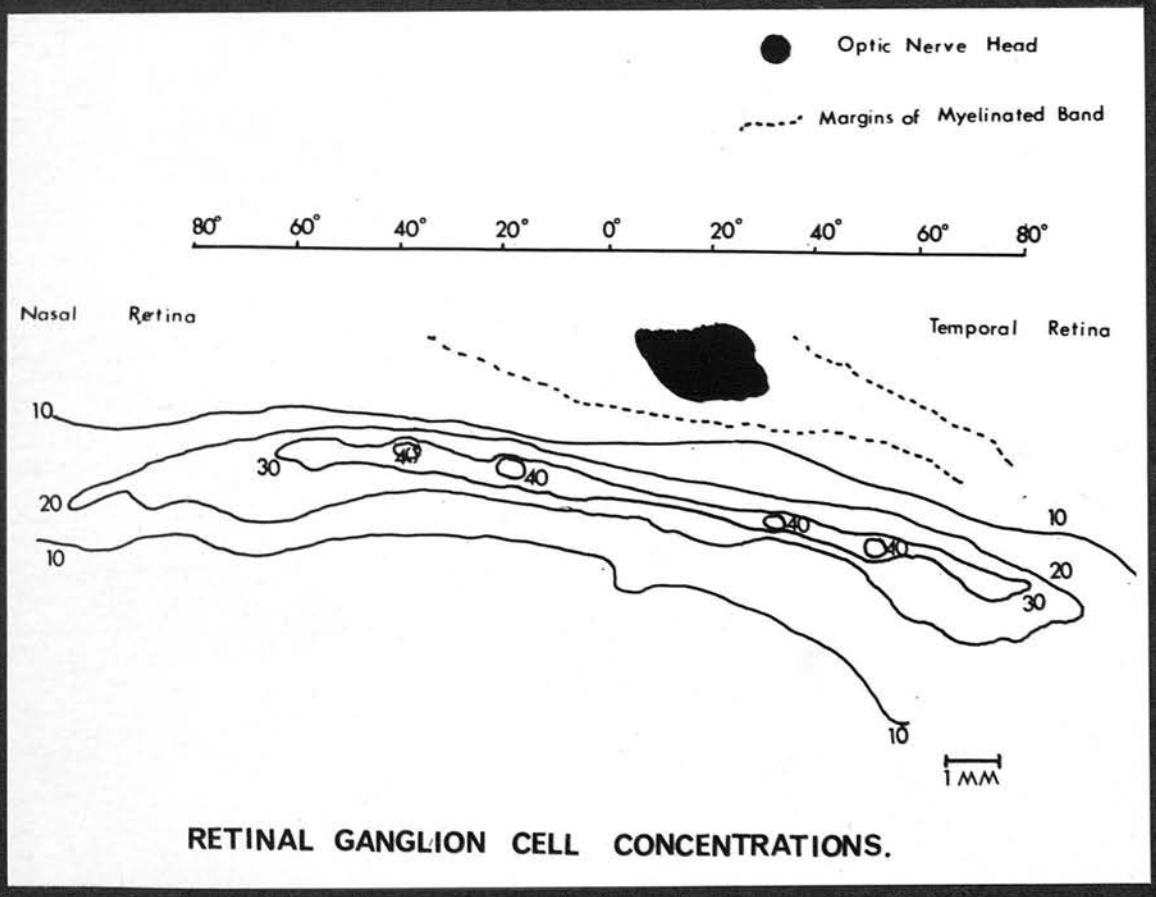

DORSAL
(b)
LATERAL
MEDIAL
270
1
2
1/2 mm
VENTRAL

Fig. 10(a) Projection of the binocular visual field on the dorsal nucleus of the lateral geniculate body.

Fig. 10(b) Retinal ganglion cells concentration 'contour'. Horizontal strip of retina, 6 mm. wide, containing optic nerve head, myelinated nerve fibre band, and the "visual streak". The figures at the end of the 'contour' line indicate the ganglion cell concentrations, in a strip of retina of unit length, i.e. 300 microns in sections 10 microns thick. (Reproduced from Seneviratne's thesis 1963).



RABBIT. BINOCULAR VISUAL FIELD



RETINAL GANGLION CELL CONCENTRATIONS.

Fig. 11 Coronal sections of the right dorsal nucleus of the lateral geniculate body showing electrode tracks.

(a) Lateral two of the three tracks passing through the antero-medial part of the dorsal nucleus.

(b) Lateral four out of five track passing through the dorsal nucleus at a coronal plane posterior to (a). These tracks are seen to extend into the ventral nucleus.

(c) Lateral three out of five tracks passing through the dorsal nucleus posterior to (b). Lateral most one extends into the ventral nucleus.

(d) Lateral two out of three tracks passing through the dorsal nucleus at a plane posterior to (c).

(e) & (f) Electrolytic lesion with the electrode track in experiments for single unit recording from the dorsal nucleus.

a
b
c
e
f

Fig. 12 Time signal = 10 and 100 m. sec. stimulus signal moves down at "on".

(a) Single unit showing "on" and "off" response

(b) Single unit showing "on" response

(c) Single unit showing "off" response

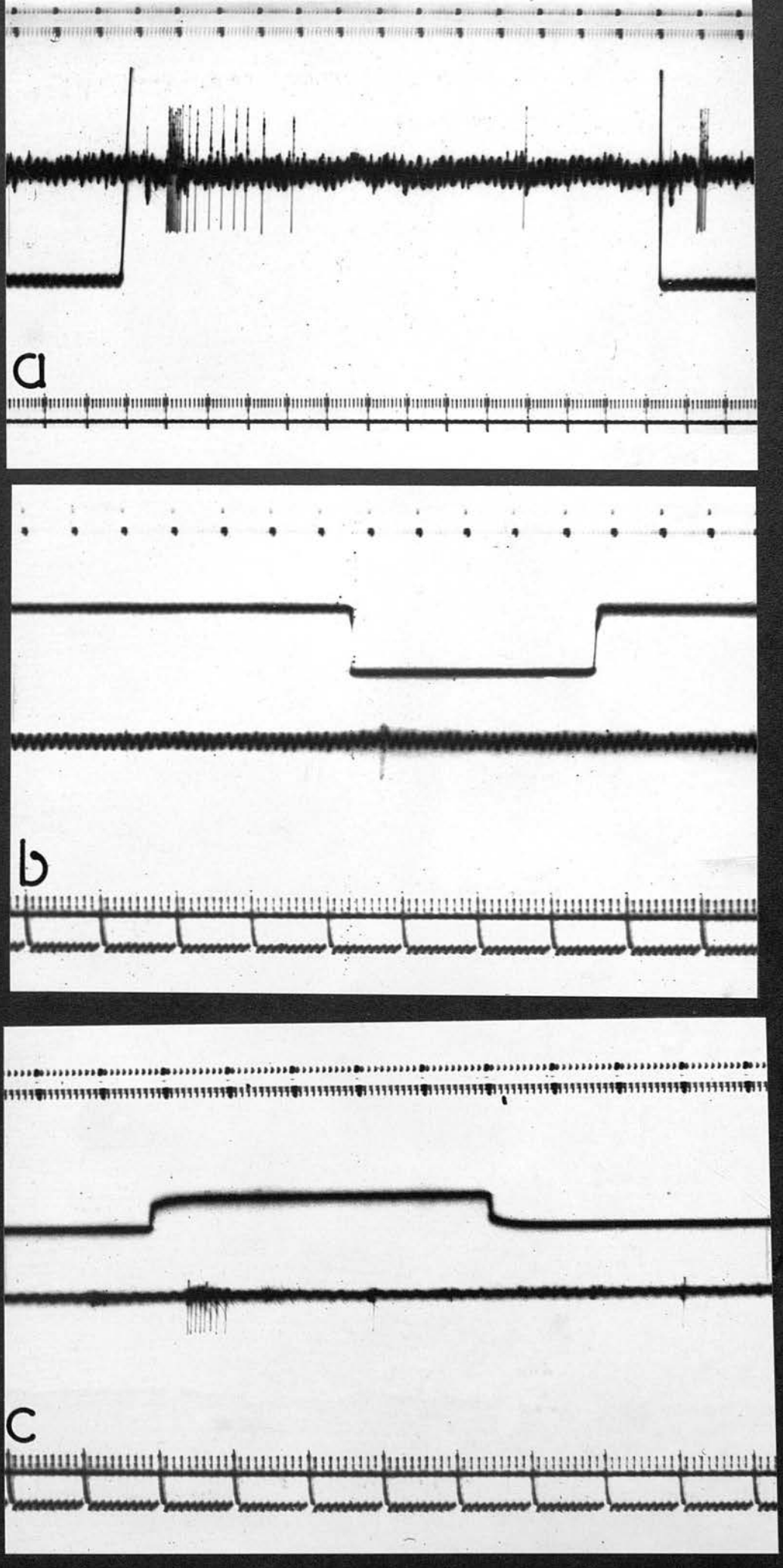
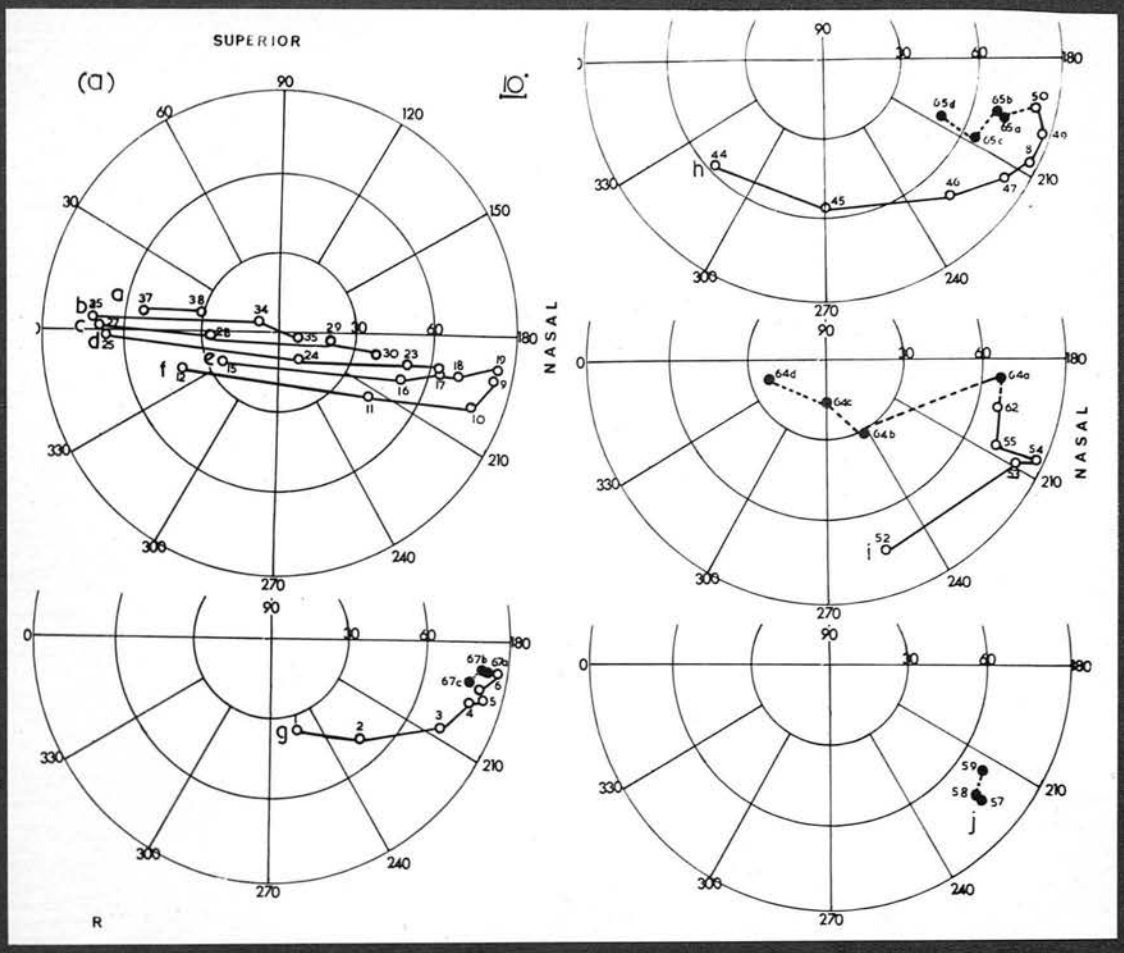

a
b
c

Fig. 13(a) Responses from the cortex localized in the visual field, in spherical-polar co-ordinates.
(Experiment RCTX 10).

Fig. 13(b) Spherical polar co-ordinates converted into parallel co-ordinates
(Experiment RCTX 10).


SUPERIOR
(a)
10°
NASAL
NASAL
R

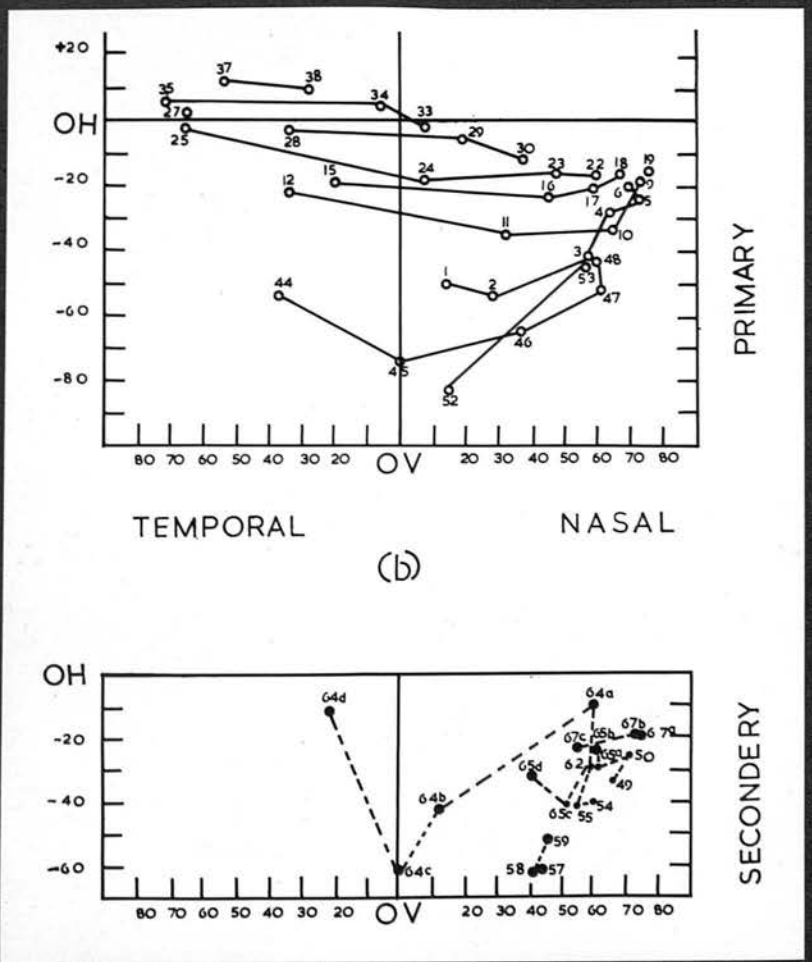

OH
-20
-40
-60
-80
OV
PRIMARY
TEMPORAL
NASAL
(b)
OH
-20
-40
-60
OV
SECONDERY

Fig. 13(c) Map of visual field projection on the cortex using parallel co-ordinates. (RCTX 10).

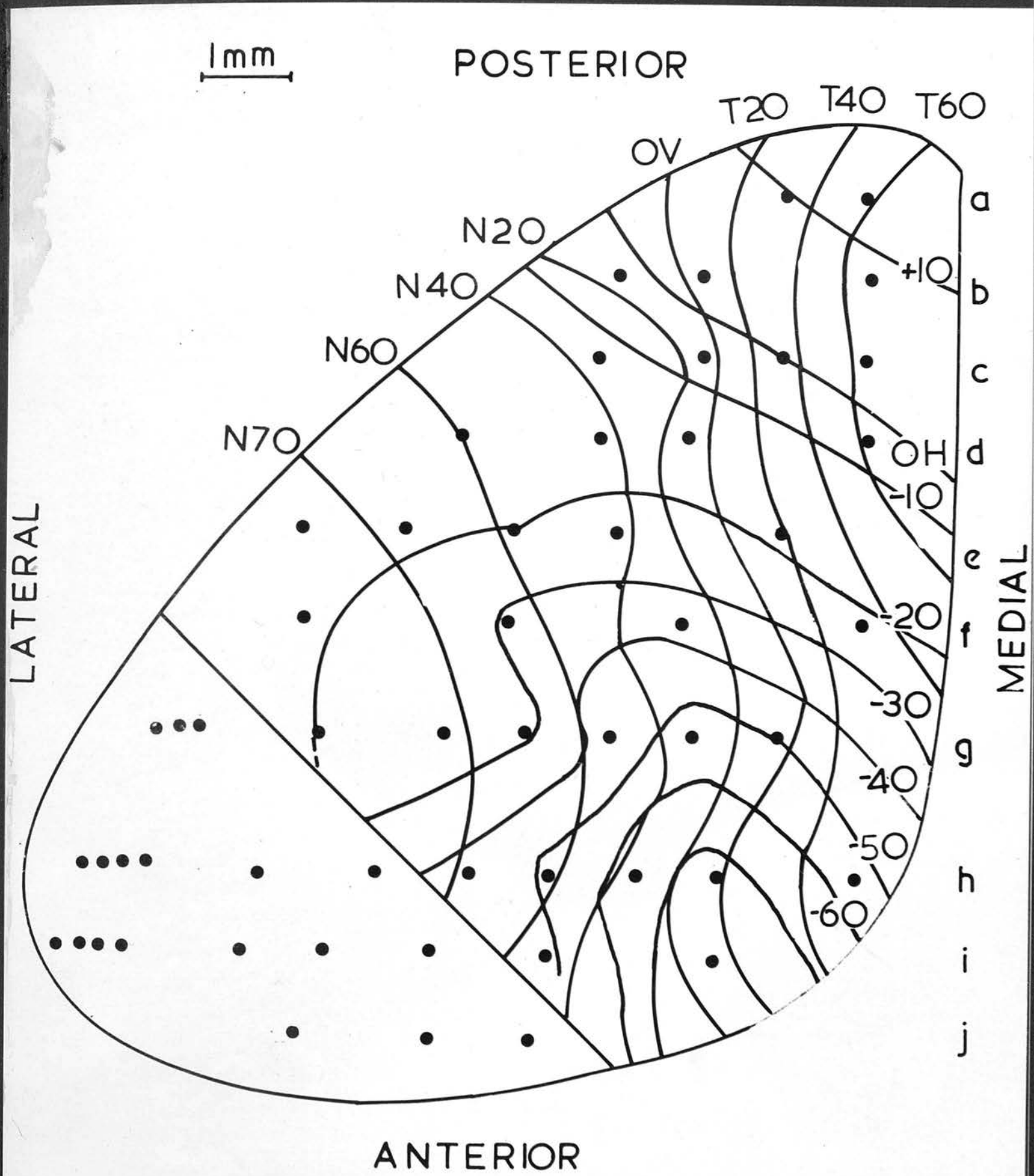
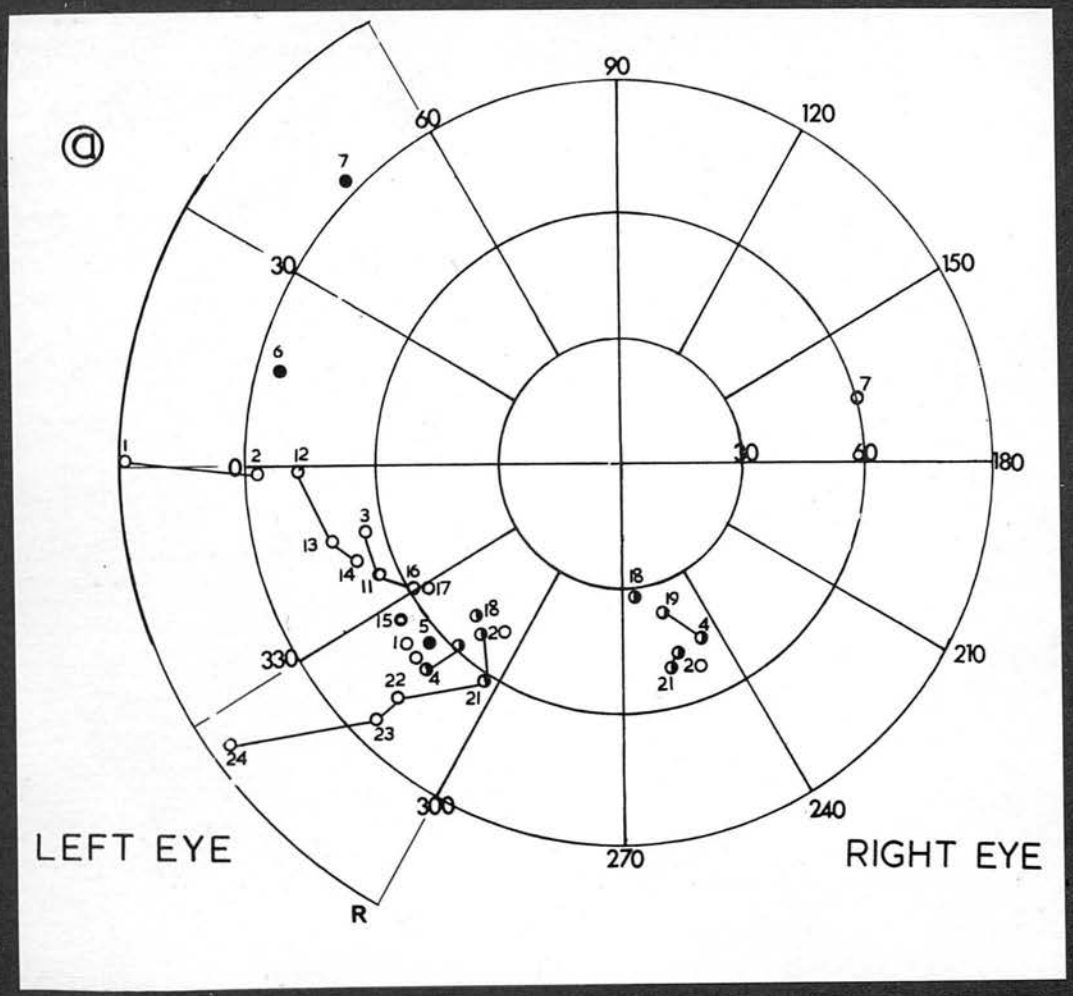
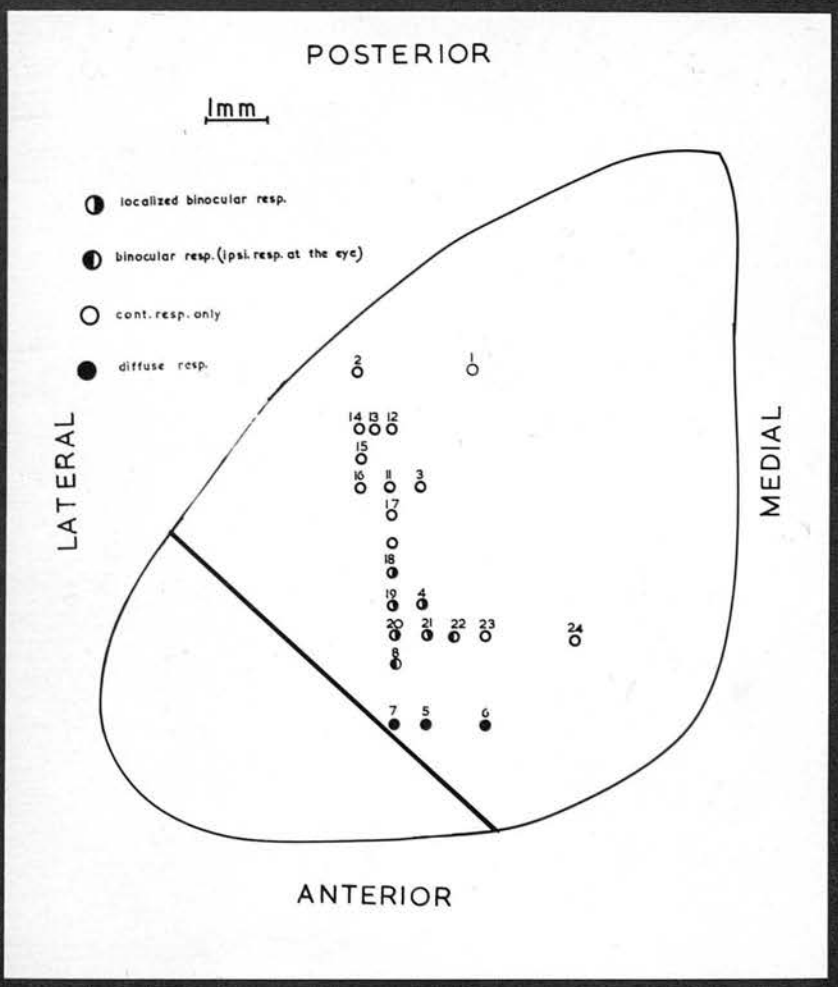

1mm
POSTERIOR
T20
T40
T60
OV
N20
N40
N60
N70
+10
OH
-10
-20
-30
-40
-50
-60
a
b
c
d
e
f
g
h
i
j
LATERAL
MEDIAL
ANTERIOR

Fig. 14(a) Perimetric localization of the binocular responses from the cortex. (RCTX 15).

Fig. 14(b) Binocular projection map on the visual cortex. (RCTX 15).


a
90
60
120
30
150
0
180
30
60
210
330
300
240
270
LEFT EYE
RIGHT EYE
R


POSTERIOR
1mm
localized binocular resp.
binocular resp. (ipsi. resp. at the eye)
cont. resp. only
diffuse resp.
LATERAL
MEDIAL
ANTERIOR

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