The Naso-Temporal Division of the Monkey's Retina

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ABSTRACT By sectioning one optic tract in each of four monkeys, and studying the distribution within each pair of retinas of the ganglion cells which remained after the affected ganglion cells had undergone retrograde degeneration, a description was obtained of the areas of a retina from which ganglion cells project to the ipsilateral and contralateral sides of the brain. Confirming previous work, ganglion cells in temporal retina were observed to project to the ipsilateral side, and cells in nasal retina to the contralateral side. It was noted, however, that ipsi- and contralaterally projecting areas of retina overlap along a vertically-oriented median strip, which is about 1° wide, and is centred on the fovea. Within this strip ipsi- and contralaterally projecting cells intermingle. Some functional implications of this result are discussed.

Each retina of the monkey projects to both ipsi- and contralateral sides of the brain (Polyak, '57; Kupfer, '63; van Buren, '63). Specifically, the ganglion cells located in the area of retina nasal to the fovea send their axons to the contralateral optic tract, and cells located temporal to the fovea send their axons to the ipsilateral optic tract. This study is an attempt to define the border between ipsi- and contralaterally projecting areas of retina. Evidence is presented that the borders of these two areas run vertically across the fovea and that the two areas overlap to a small but significant degree. As in the cat (Stone, '66), a *median strip of overlap* can be described within which ganglion cells which project to ipsi- and contralateral optic tracts intermingle. The strip runs vertically in the retina, passing across the fovea. In the monkeys used (*Macacca irus*) its width ranged from 150–250 μm. This corresponds to approximately 1° of visual angle.

METHODS

The experimental approach was basically that used for the cat (Stone, '66). Four monkeys (*Macacca irus*) were used. In each one optic tract was sectioned by aseptic surgery under pentobarbitone anaesthesia. The approach was through the temporal bone, with the animal lying on its side. The tip of the temporal lobe was removed by suction (fig. 1) allowing visualization of the optic nerve, chiasm and tract. A hook was passed under the tract and pulled upwards, dividing it. Surgery was performed in adult or young adult (2-year-old) monkeys.

Following survival times of 6 to 12 months the monkeys were anaesthetized and perfused through the heart with 0.9% saline followed by 10% formol-saline. Two animals were, before perfusion, placed in a stereotaxic apparatus, paralyzed by intravenous injection of gallamine triethiodide (Flaxedil) and artificially respired. Their fundi were photographed using a Zeiss fundus camera, and the optic disc and fovea of each retina were projected onto a frontal 1 metre tangent screen, using techniques described previously (Bishop, Henry and Smith, '71). Following perfusion the eyes of each animal were enucleated and the brain removed. The eyes of the two animals whose fundi had been photographed were placed in saline and photographed with eyeball gently inflated. These photographs allowed estimation of the radii of curvature of the cornea and eyeball and of the length of the eyeball. The opened fundus of each of these

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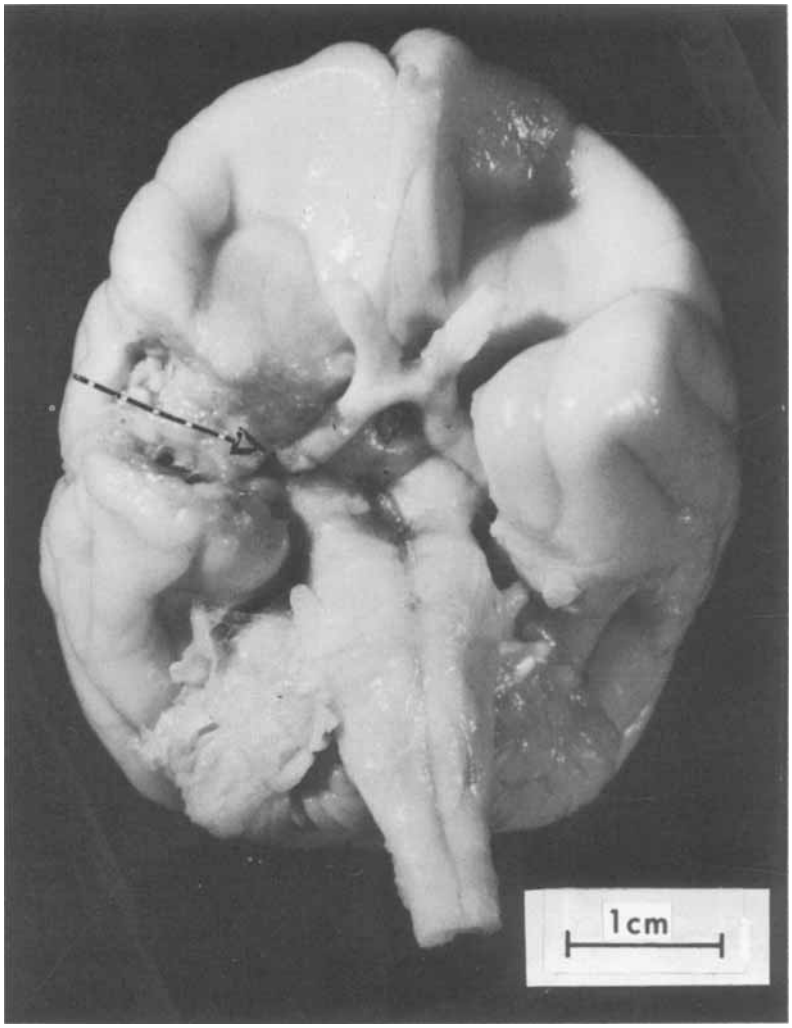


Fig. 1 Ventral surface of brain of tract-sectioned monkey. The dotted line marks the surgical approach, through the right temporal lobe. The arrow points to the peripheral stump of the right optic tract.

four eyes was subsequently photographed (fig. 10).

Methylene blue-stained whole mounts of the retinas were prepared as follows. Each eye was cut around so that the anterior part (lens, ciliary body, iris and cornea) was separated from the posterior, fundal part. The anterior part was discarded and the posterior half placed in 10% formol-saline for two days. The posterior half of each eye was then cut into appropriate pieces. Particular attention was given to the central piece, which was always cut to include the optic disc and the fovea, but the peripheral pieces were also mounted and stained. The staining technique was a modification of that described previously (Stone, '65, '66) for retinal whole mounts. It is somewhat simpler than the earlier techniques, and has proved entirely reliable. The preparations have now lasted two years without deterioration, and appear likely to last indefinitely. Each piece of retina was dissected free of the choroid. In the central piece the optic nerve was cut with the tip of a scalpel blade passed between retina and choroid. Each piece of retina was cleaned as completely as pos-

sible of pieces of choroid clinging to its outer surface and of the vitreous humour attached to its inner surface. The piece was then laid, fibre layer uppermost, on a gelatinized glass slide and processed through the following steps:

1. Each preparation (i.e., each piece of retina spread on a gelatinized glass slide) was placed in hot (60°C) formalin vapour for two hours, so that the retina stuck firmly on the slide. The remaining steps were done at room temperature.

2. The preparation was washed briefly in distilled water, and then stained by laying the retina "face-down" over a small Petrie dish brimming with 0.2% methylene blue. This face-down contact of retina with stain minimized the precipitation of particles of stain onto the retinal surface. Three minutes staining time at room temperature reliably gave an appropriate depth of stain, but this can be monitored under a microscope.

3. Excess stain was wiped off and the stain was fixed in 5% ammonium molybdate (3 minutes).

4. The preparation was washed in distilled water, then dehydrated and cleared by placing for three minutes in each of the following solutions: 90% alcohol, absolute alcohol (2 changes) and xylol (2 changes).

5. Depex was used for mounting.

This sequence is equally effective for staining cat and rabbit retina; we commonly processed a piece of cat retina immediately before the monkey retinas, to check for defective solutions.

RESULTS

Optic tract sections

Figure 1 shows the appearance of the ventral surface of the brain of one tract-sectioned subject. The arrow follows the surgical approach through the temporal lobe and points to the stump of the severed optic tract. Essentially identical controls of the tract section were obtained in the other animals.

Normal retina

In the normal monkey retina, seen in a whole mount preparation (fig. 2), the foveola is a circular area about 500 μm in diameter, which is surrounded by densely

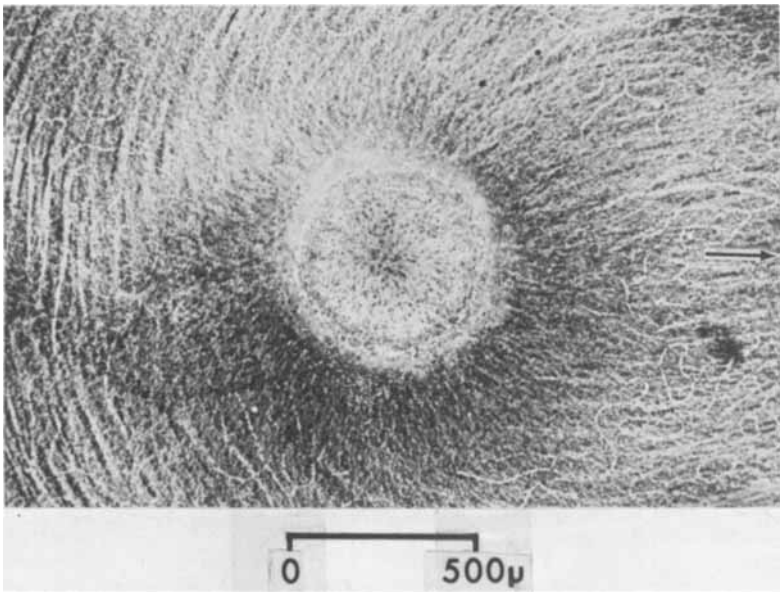


Fig. 2 Foveal area of the right retina of a normal *Macacca irus* seen in a methylene blue-stained whole mount. The pale circle in the centre of the field is the foveola, i.e. the area free of ganglion and bipolar cells. The ganglion cells form a continuous layer, several deep, surrounding the foveola. The paths of axon bundles and of small blood vessels are apparent as faint streaks and loops. The arrow points to the optic disc.

packed ganglion cells (see also fig. 10 in Stone, '65). Pale streaks are apparent running across the surface of the ganglion cell layer and revealing the pattern of fibre bundles around the foveola (cf. fig. 162 in Poliak, '57). The streaks mark the paths of fibre bundles. They appear because the fibre bundles limit access of the stain to the underlying ganglion cells. The more tortuous pale lines are the paths of superficial blood vessels.

The retinal distributions of ipsi- and contralaterally projecting ganglion cells: basic observations

Confirming previous observations in monkey and man (Gartner, '51; Kupfer, '63; van Buren, '63) ganglion cells in the temporal half of the retina ipsilateral to the tract section and in the nasal half of the contralateral retina underwent retrograde degeneration. Figure 3A shows at low power the appearance of a methylene blue stained whole mount of the right (ipsilateral) retina of one monkey, six months following section of the right optic tract. Up on the figure is "up" on the retina and left on the figure is "temporal" on the retina; i.e. the retina is "looking at" the reader. This convention is followed in all relevant drawings and illustrations. The fovea is in the centre of the illustration and the surrounding retina can clearly be divided into the lighter, temporal (left) half, in which the ganglion cells have degenerated and disappeared and the darker, nasal (right) half in which ganglion cells appear to be present in normal numbers. Figure 3B shows the appearance of the left retina of the same animal. It is equally clearly divided into areas lacking and containing ganglion cells. Figures 4A and B show the foveal areas of these retinas at higher magnification. In each retina the boundary of the area containing ganglion cells is an approximately straight line which passes slightly to one side of the midpoint of the foveola. The line can be considered to run vertically because it runs perpendicular to the line joining the fovea to the disc (see figs. 3, 10). This latter line runs horizontally, as assessed ophthalmoscopically, and by projection of retinal landmarks in the paralyzed animal (table 1).

Figure 5 shows, at still higher power, areas of the ganglion cell layer at the junction of normal and degenerated areas. Figure 5A shows an area at the upper margin of the foveola (labelled F) of the right retina shown in figures 3A and 4A. Figure 5B shows an area at the lower margin of the foveola of the left retina shown in figures 3B and 4B. In each of figures 5A and 5B a sharp gradient in ganglion cell density is apparent. Many cell bodies are nevertheless apparent in areas lacking ganglion cells; their significance is considered further below.

Figures 6 and 7 show the whole mounts obtained from two other animals. In each eye the line dividing normal and degenerated retinal areas could be traced for 2 to 3 mm above and below the fovea. Because the line is formed by ganglion cells it becomes less distinct towards the retinal periphery, as the density of ganglion cells decreases.

The overlap

In micrographs such as figures 3, 4, 6 and 7 it is reasonably straightforward to delineate the areas of retina which contain ipsi- and contralaterally projecting ganglion cells. Do these areas overlap in one retina? Figure 8A was traced from the right retina in figure 4A. The foveola is outlined, the area containing ganglion cells is hatched and its temporal limit is drawn as a line. Figure 8B is the analogous tracing obtained from the left retina in figure 4B. Figure 8C is figure 8B reversed left-to-right. Figure 8A then represents the area of a right retina containing *contralaterally projecting* ganglion cells, and figure 8C represents the area of a right retina containing *ipsilaterally projecting* cells. When figures 8A and 8C are superimposed, with the outlines of the foveolae superimposed as closely as possible, figure 8D is obtained. The areas of ipsi- and contralaterally projecting cells appear to overlap along a narrow (approximately 150 μm wide) vertical strip which runs across the centre of the fovea. Figures 9A, B, C show the strip of overlap of ipsi- and contralaterally projecting areas of retina obtained in three other monkeys. The strip is clearly analogous to the median strip of overlap described in the cat's retina (Stone, '66).

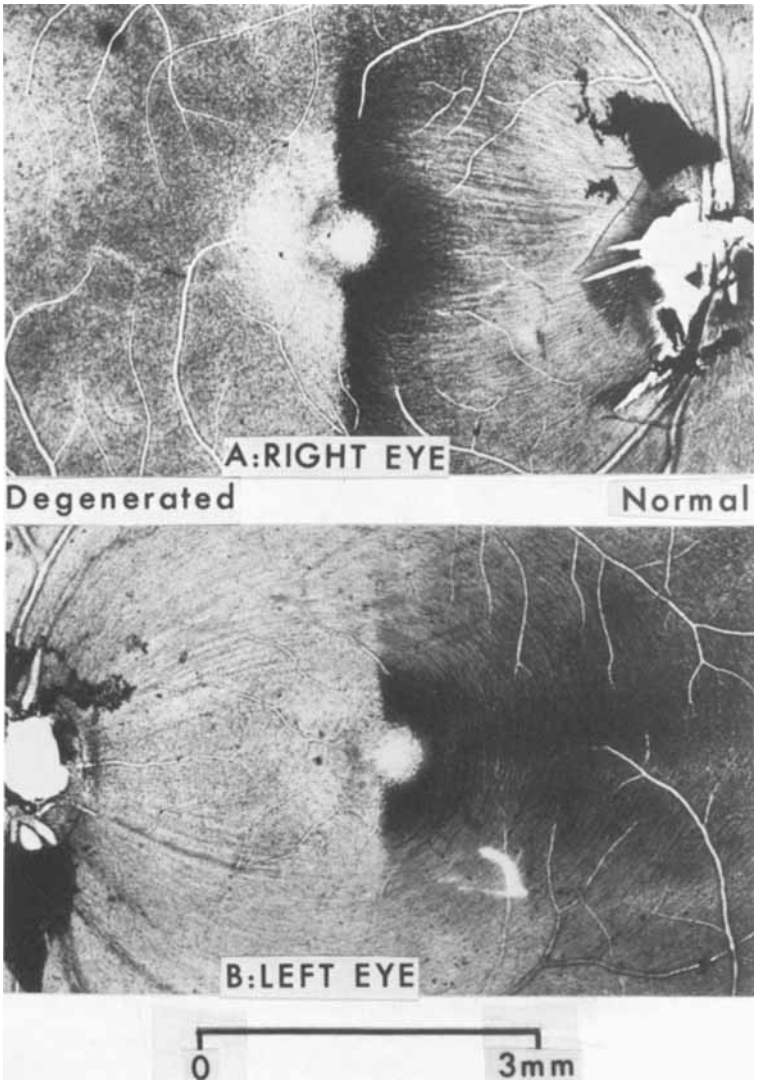
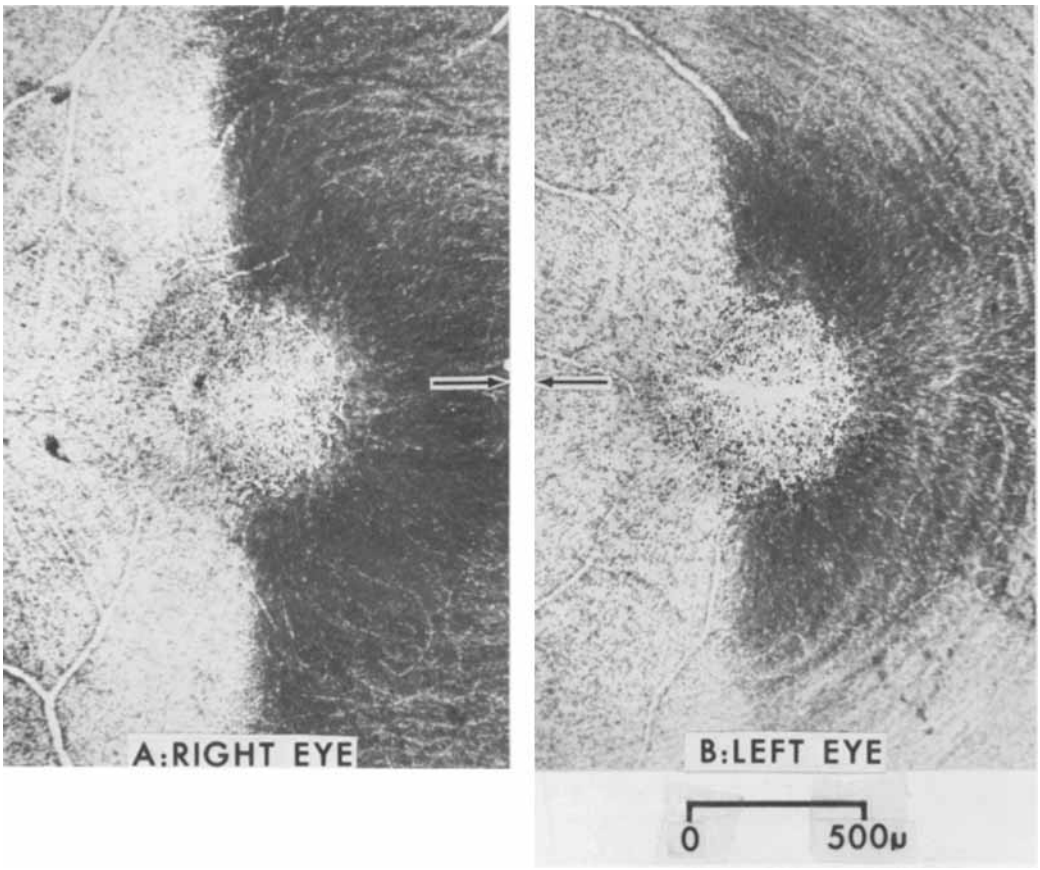


Fig. 3 Retinas of one tract-sectioned monkey seen in methylene blue whole mounts. A: Right retina: The fovea is at the centre of the photograph and the optic disc is the torn patch at right, from which blood vessels and axon bundles radiate. The area of retina temporal to (to the left of) the fovea is lacking ganglion cells and has stained relatively lightly. The area of retina nasal to (to the right of) the fovea has a normal population of ganglion cells, and has stained more darkly. The border between the two areas is a straight line which runs vertically in the retina, crossing the fovea. The border runs perpendicular to the line joining fovea to the centre of the optic disc. B: Left retina: The fovea is at the centre of the figure and the optic disc is at left. Ganglion cells are lacking from the area of retina nasal to the fovea and are present in the area temporal to the fovea. The border between these two areas is a straight line which runs vertically in the retina, crossing the fovea. In both left and right retinas the border between areas containing the lacking ganglion cells runs slightly *to the left* of the centre of the foveola. For further interpretation, see text.



Figs. 4A,B Foveal regions of the retinas of figure 3A,B respectively, at higher magnification. In each retina the arrow points to the optic disc.

Ophthalmoscopic and post-mortem appearance of the fundus

Ophthalmoscopically the only suggestion of abnormality was a sheen on the areas of retina from which ganglion cells had degenerated. This was more apparent in the right retina, in which the temporal half of the retina was affected. The area of sheen appeared to include the lateral margin of the fovea.

When the eye was opened post-mortem clear indication of the pattern of ganglion cell degeneration was apparent, even before staining (fig. 10). The retina appeared "milky" and opaque where it was normal, and was more transparent, making the fundus appear darker, where the ganglion cells had degenerated. The impression was gained that the relative transparency of the retinal areas affected by degeneration is due to the absence of axon bundles from such areas. In the right retina (fig. 10A) the fibre bundles form a continuous layer of axons as they converge on the optic disc, as in the normal retina, but the bundles begin to form only nasal to the fovea. A clear line between normal (nasal) and degenerated (temporal) areas of retina is apparent for 2–3 mm above and below the fovea. In the left retina (fig. 10B), the axon bundles all arise from ganglion cells in temporal retina and form two arcuate streams which course above and below the disc-fovea line. A clear line between normal (temporal) and degenerated (nasal) areas of retina is apparent for only about 1 mm above and below the fovea. Further up and down axon bundles cross the line, obscuring it. The same effect is seen in the stained retina (fig. 3B), be-

TABLE 1

Parameters of monkey eyes

	Monkey 1		Monkey 2	
	Left eye	Right eye	Left eye	Right eye
Optic disc:				
Vertical axis	1.6 mm, 8.4°	1.6 mm, 8.0°	1.45 mm, 7.5°	1.45 mm, 8.0°
Horiz. axis	1.0 mm, 5.2°	1.15 mm, 5.6°	1.0 mm, 5.2°	1.10 mm, 5.9°
Disc centre to fovea	3.2 mm, 18°	3.2 mm, 16°	3.2 mm, 18°	3.25 mm, 18°
PND (range)	11.1 mm (10.4–11.9 mm)	11.5 mm (11.3–11.6 mm)	11.0 mm (10.5–11.4 mm)	10.5 mm (10.2–10.7 mm)
Radius of corneal curvature	5.2 mm	5.2 mm	5.5 mm	5.5 mm
Antero-post. length of eyeball	17.5 mm	17.5 mm	17.0 mm	17.0 mm
Angle between the horizontal and the line joining blind-spot to fovea, in paralyzed animal	3°	1°	4°	3°

cause the axon bundles, although they do not stain, reduce the access of the stain to the underlying ganglion cells.

Are there contralaterally projecting cells in temporal retina?

Stone ('66) concluded that in the cat 25% of the ganglion cells of temporal retina project to the contralateral optic tract, and the presence of contralaterally projecting cells in temporal retina in the cat has been confirmed physiologically (Ogawa et al., '69; Fukada, '71). Such cells do not appear to be present in the monkey retina. Figures 11a,d show respectively the nasal (degenerated) margin of the left foveola and the temporal (degenerated) margin of the right foveola, from one monkey. Numerous cell bodies remain in both areas but evidence is presented below that few, if any, are ganglion cell bodies. Importantly, the impression is not gained that, as in the cat, there are more and larger cell bodies remaining in the temporal area. The same similarity is apparent (figs. 11b,c,e,f) between peripheral areas of nasal and temporal retina (both degenerated).

Observations on the cells remaining in the ganglion cell layer after tract section

It was important to test whether the cells which remained in the ganglion cell layer, in areas of retina such as those illustrated in figure 11 included ganglion cells whose axons somehow escaped section. Many of these remaining cells are much smaller than ganglion cells but some are of comparable size. Figure 11 shows a comparison of degenerating areas of nasal retina (upper row) and temporal retina (lower row). The areas in figures 11a and d are on the margin of the foveola; the areas in b and e are 2.0 mm from the fovea; the areas in c and f are 5.0 mm from the fovea. The density of cells does not decrease consistently with the increasing distance from the fovea, as might be expected if a considerable proportion of the cells were ganglion cells. Interestingly, the highest density of cells is in the area in figure 11e. This area is 2.0 mm nasal to the fovea, and hence about 0.5 mm from the edge of the optic disc. The higher density of cell bodies in this area can be explained by the assumption that these are the bodies of

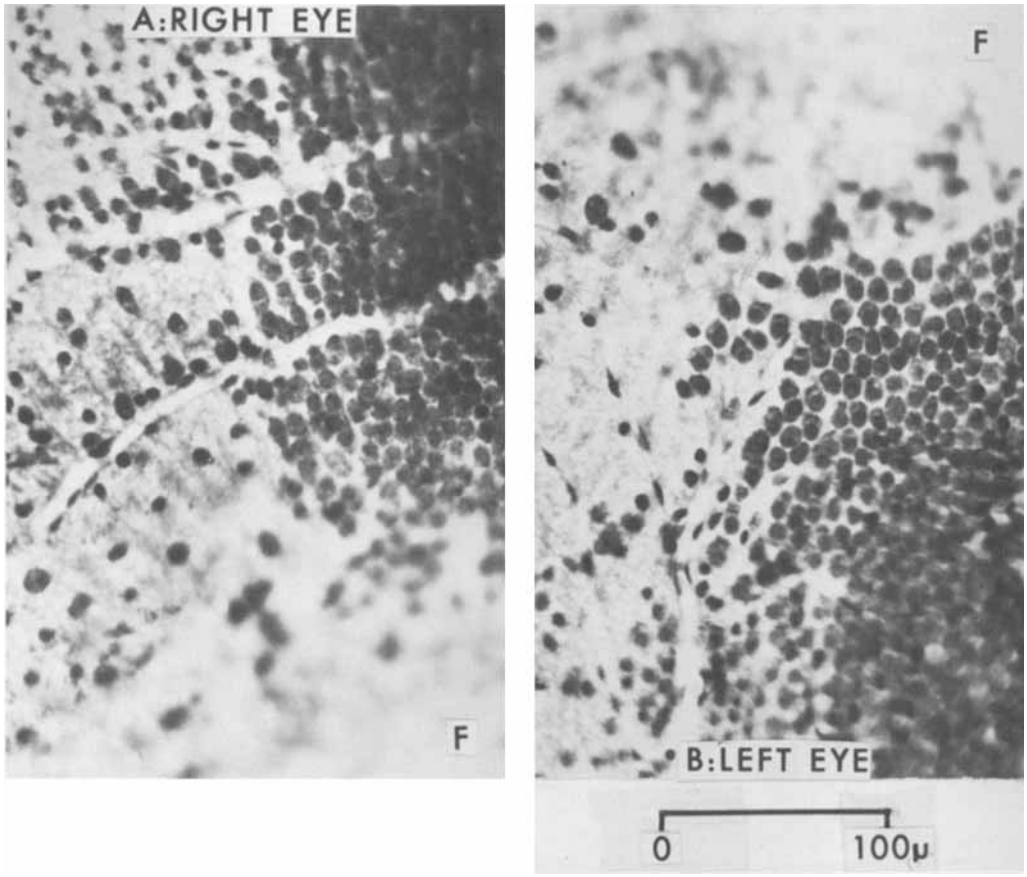
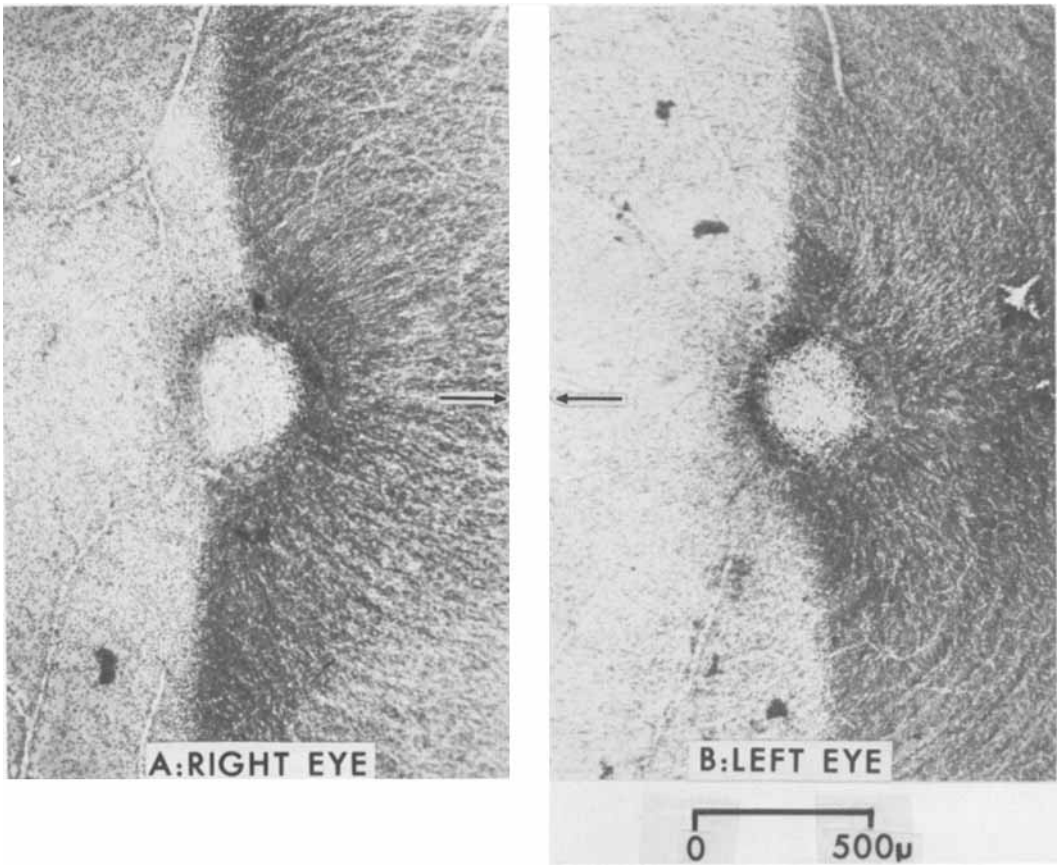


Fig. 5 A: Area at the upper margin of the fovea of the retina in figures 3A and 4A, at higher magnification. The plane of focus is at the ganglion cell layer, showing the gradient in ganglion cell density in this region. B: Area at the lower margin of the fovea of the retina in figures 3B and 4B. The plane of focus is at the ganglion cell layer. The letters F mark the position of the edge of the foveola, in each of A and B.

neuroglial cells, which increase in number near the optic disc to provide support for the axon bundles of the fibre layer, which reaches its maximal thickness near the disc. A second test of the nature of the cells which remain in the ganglion cell layer after tract section would be provided by comparison with a retina from which all ganglion cells had degenerated, following optic nerve section. Towards the end of the present study, optic nerve section was attempted in two animals. One animal survived surgery but, when examined six months later, the section proved incomplete. A further attempt at complete nerve section has been made and will be reported elsewhere.

Appearance of the retina in sections

One retina (that shown in whole mount in fig. 7A) was carefully detached from the slide with a razor blade, embedded in celloidin, sectioned and restained with cresyl violet (the methylene blue was washed out by various alcohols). On the unaffected side of the retina the ganglion cell, inner nuclear and outer nuclear layers are clearly visible both at the fovea (fig. 12B) and 5 mm away (fig. 12D). On the side affected by tract section the number of cell bodies in the ganglion cell layer is dramatically reduced (fig. 12A, C). The inner and outer nuclear layers appear normal.



Figs. 6A,B Right and left retinas respectively of a second monkey, presented in the same format and at the same magnification as figure 4.

Physical dimensions of the monkeys' eyes

Two animals were paralyzed before perfusion and fixed in a stereotaxic headholder facing a tangent screen 1 m from the eye. The boundaries of the optic disc of each eye were then projected onto the tangent screen, giving an outline of the blind spot. The centre of the fovea was similarly projected giving the position of the fixation point. In these two animals several dimensions of the eyes were measured, from photographs of the eyes taken immediately post-mortem. These dimensions were the antero-posterior length of the eyeball, the radius of corneal curvature, the size of the optic disc and the distance between the centre of the disc and the fovea. These measurements are tabulated in table 1.

To a close approximation the posterior nodal distance (PND) of the eye is given by (Vakkur, Bishop and Kozak, '63)

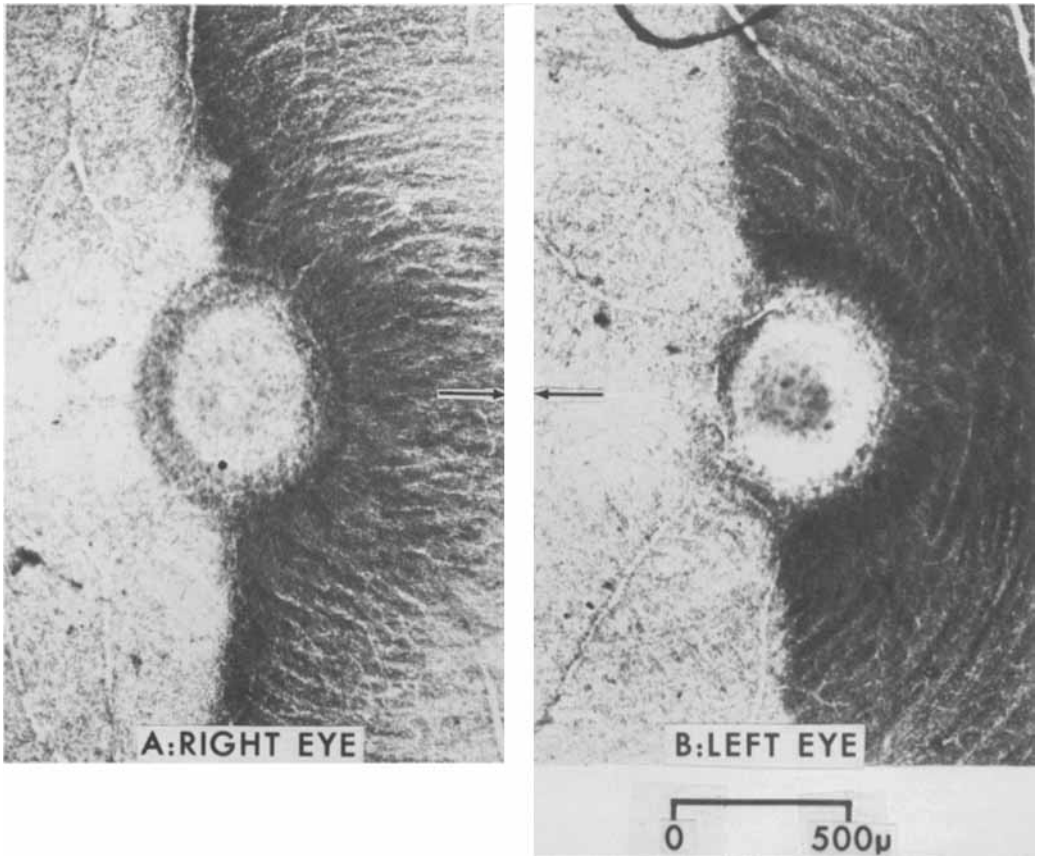
$$PND = T \times d/D$$

where T is the distance from the anterior nodal point of the eye to the tangent screen (1 m);

D is a dimension on the tangent screen (say the distance from the projection of the fovea to the centre of the blind spot) and

d is the corresponding distance on the retina (i.e., the distance from the fovea to the centre of the optic disc).

For each eye three estimates of the PND were made, one using the disc-fovea distance, and the other two using the vertical and horizontal axes of the disc. The mean and range of values for each eye are given



Figs. 7A,B Right and left retinas respectively of a third monkey, presented in the same format and at the same magnification as figures 4 and 6.

in table 1. For all four eyes the mean PND was 11.0 mm and the range 10.2 mm to 11.9 mm.

From the posterior nodal distance the angle subtended by the strip of overlap can be calculated. As already noted the strip, as estimated here, varies in width from animal to animal, and with position in any given animal. In the schematic diagrams in figures 8D and 9 the strip varies in width approximately from 0.5° to 1.25°. Considering the errors inherent in this measurement (see DISCUSSION) it seems a reasonable approximation to state the strip of overlap is about 1° wide.

Shrinkage of whole mount preparations

In a previous study (Stone, '66) it was estimated that the shrinkage of the retina during processing of the whole mount preparations was 5% of length or less. This estimate was confirmed in the preparations made in this study. For example, the distance between the centre of the optic disc and the fovea was measured in two animals (4 eyes) with the retina in situ, after the cornea and lens had been removed (fig. 10). This distance ranged from 3.20 to 3.25 mm (table 1). In the whole mount preparations of these retinas, this distance ranged from 3.1 mm to 3.2 mm (e.g., fig. 3).

DISCUSSION

Sources of error

Two sources of error in the estimation of the width of the strip of overlap must

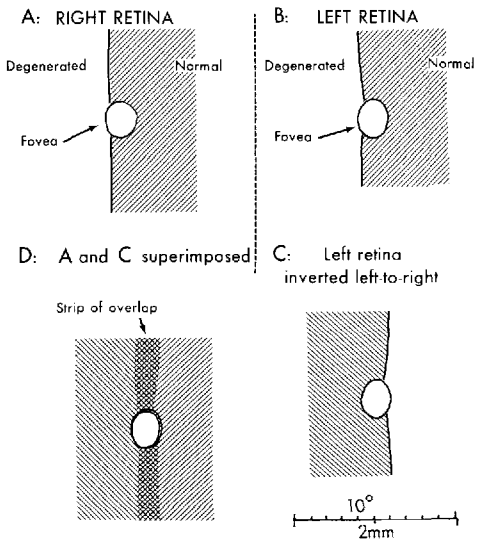


Fig. 8 A: Schematic drawing of the foveal region of the right retina in figure 3A. The outline of the foveola is drawn in and the areas lacking and containing ganglion cells are open and hatched, respectively. The border between these two areas is marked as a line. B: Analogous drawing for the left retina of the same animal. C: The drawing in B reversed left-to-right. D: A and C superimposed. The outlines of the foveolae are matched as closely as possible and the lines are made as close to parallel as possible. This figure gives an estimate of the strip of overlap, marked here with double hatching.

be stated. First, the retina *in vivo* approximates in shape the surface of a sphere. Consequently, the retina is necessarily distorted somewhat as it is flattened onto a glass slide. This distortion was minimized by keeping the piece of retina containing the optic disc and fovea fairly small (typically 9 mm × 9 mm), but could not be eliminated. This has presumably caused some distortion in the shape of the strips of overlap shown in figures 8 and 9. Second, there is presumably some small error in figures 8 and 9 in the placement of the borders of the areas containing ganglion cells. However, although these two factors clearly limit the accuracy with which the width of the strip of overlap can be estimated, neither seems sufficient to qualify the conclusion that there is a strip of overlap, within which ipsi- and contralaterally projecting ganglion cells intermingle. The strip runs vertically in the retina, and is centered on the fovea. It is approximately 1° wide.

Degree of functional overlap

The present study describes only the retinal distributions of ipsi- and contralaterally projecting ganglion cells. Thus the overlap described is an overlap of the areas of retina which contain contra- and ipsilaterally projecting ganglion cells. What is the functional overlap? That is, how wide is the overlap of ipsi- and contralaterally projecting receptors? Morphological studies (see for example, plate 34 in Boycott and Dowling, '69) indicate that, except at the fovea, the processes of receptor and bipolar cells run radially through the thickness of the retina, connecting the ganglion cells to the receptors immediately external to them. It seems likely, therefore, that the overlap of ipsi- and contralaterally projecting cells is at least as wide in the receptor layer as in the ganglion cell layer. The overlap may be somewhat wider in the receptor layer, since many ganglion cells may have receptive fields larger than their cell bodies.

The problem of overlap at the fovea

The presence of the fovea in monkey retina made it relatively simple to demonstrate the presence of a strip of overlap. The task was certainly simpler than in the cat retina, where it was necessary to quantify ganglion cell density. (Conversely the high density and multilayering of ganglion cells up to 8 mm from the monkey fovea (van Buren, '63) makes the counting approach used in the cat impractical in the monkey). However, because the ganglion cells connected to receptors within the foveola are displaced from those receptors, the present study does not test whether there is overlap within the foveola. It does demonstrate that the strip of overlap in the ganglion cell layer runs, apparently without distortion, across the superior and inferior margins of the fovea, which contain ganglion cells displaced upwards and downwards, respectively, from the foveola. It does also demonstrate that contralaterally-projecting ganglion cells are displaced to the nasal margin of the foveola, and ipsilaterally-projecting cells to the tem-

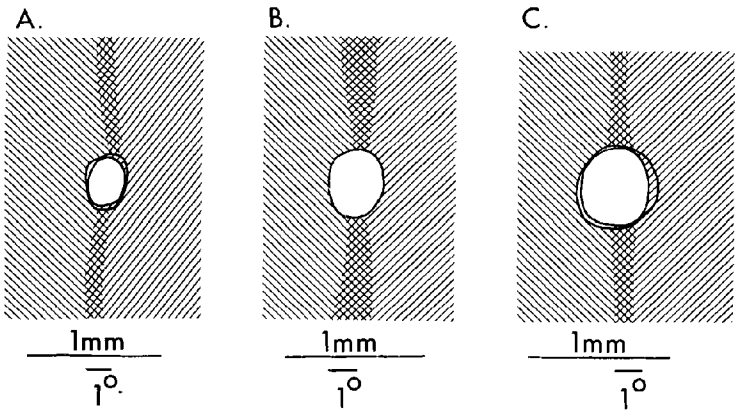


Fig. 9 Drawings like that in figure 8D for three other monkeys. In each the strip of overlap is represented by the double-hatching.

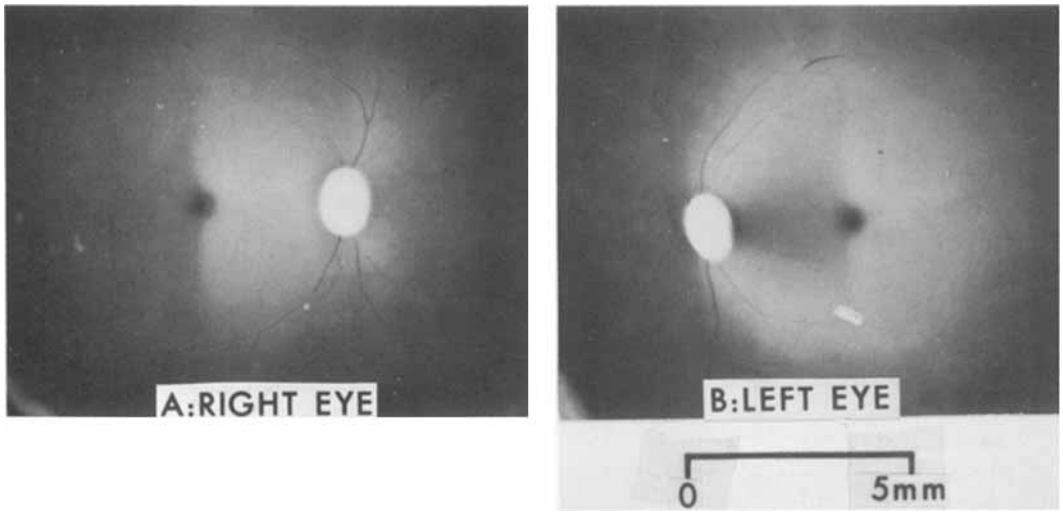


Fig. 10 The appearance of the fundi of the right (A) and left (B) eyes of one monkey, immediately after perfusion. The stained retinae of these two eyes are shown in figures 3, 4 and 5. In each fundus the foveola is the dark spot at the centre of the figure. The optic disc is the white ellipse from which blood vessels radiate.

poral margin. But because it is an analysis of the positions of ganglion cell bodies the present approach cannot demonstrate overlap within the foveola.

It is, of course, conceptually economical to assume that there is no functional discontinuity at the foveola in the overlap of ipsi- and contralaterally projecting areas of retina, and this assumption is made in the following discussion. It may however be important to keep in mind that it is an assumption.

Functional significance

Linksz ('52) argued that ipsi- and contralaterally projecting areas of human retina must overlap, since a precise, non-overlapping wiring would be biologically unlikely. Ogle ('62) argued for the presence of an overlap, on the grounds that Panum's area shows no discontinuity at the fixation point. Both workers recognized that the overlap might be too small to be detectable by perimetry. The present study seems to confirm their ideas.

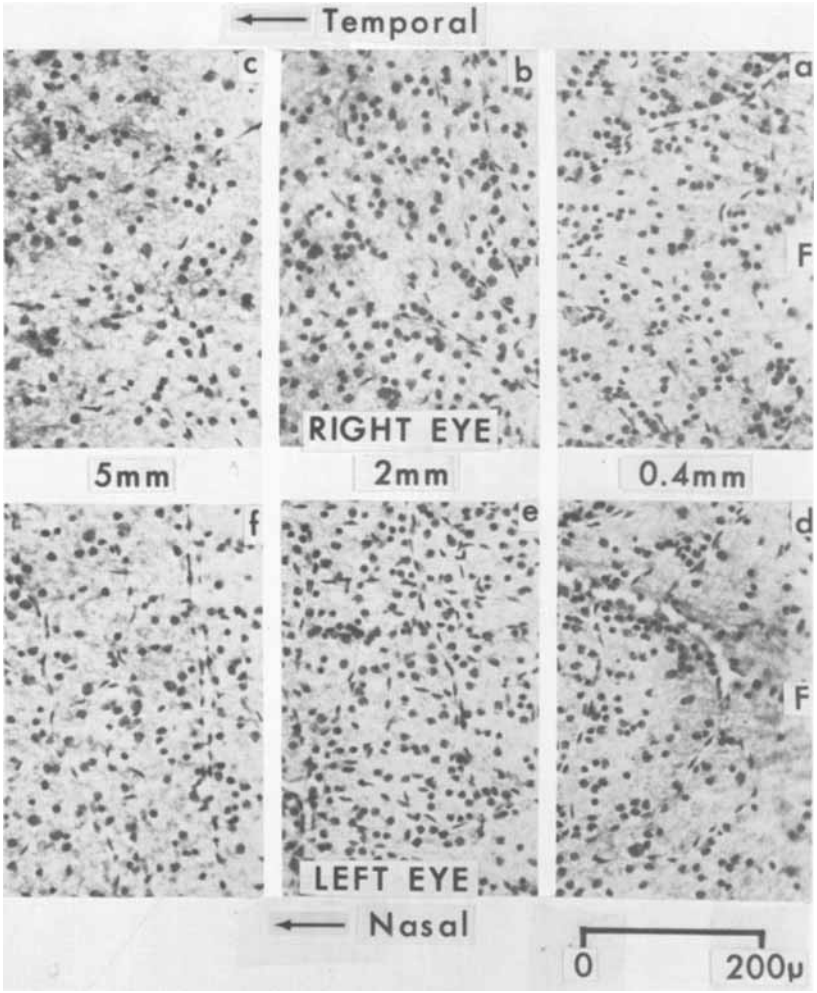


Fig. 11 Upper row (a,b,c): Areas from the right retina of a monkey in which the right optic tract was sectioned (same retina as in figs. 3A, 4A, 5A). Figure 11a shows an area on the margin of the foveola 0.4 mm temporal to the centre of the foveola; b shows an area 2 mm temporal to the centre of the foveola; c shows an area 5 mm temporal. Lower row (d,e,f): Areas from the left retina of the same animal (same retina as in figs. 3B, 4B, 5B). Figure 11d shows an area on the nasal margin of the foveola; e shows an area 2 mm nasal; f shows an area 5 mm nasal.

The presence of a central, vertically-running strip of retina which projects to both hemispheres has become important in recent theories of the neurophysiological basis of binocular depth discrimination (Blakemore, '69; Bishop, '70). These theories were developed from studies of receptive field disparity in cat visual cortex. The present finding that a strip of overlap of similar width is present in the monkey suggests that these theories may be equally valid for the monkey, and perhaps for man.

Finally, the possibility must be considered that the overlap of ipsi- and contralaterally projecting areas of retina might form a basis for macular sparing. Although the present results suggest that more than half the fovea is functional after tract section, considerable difficulties arise in any

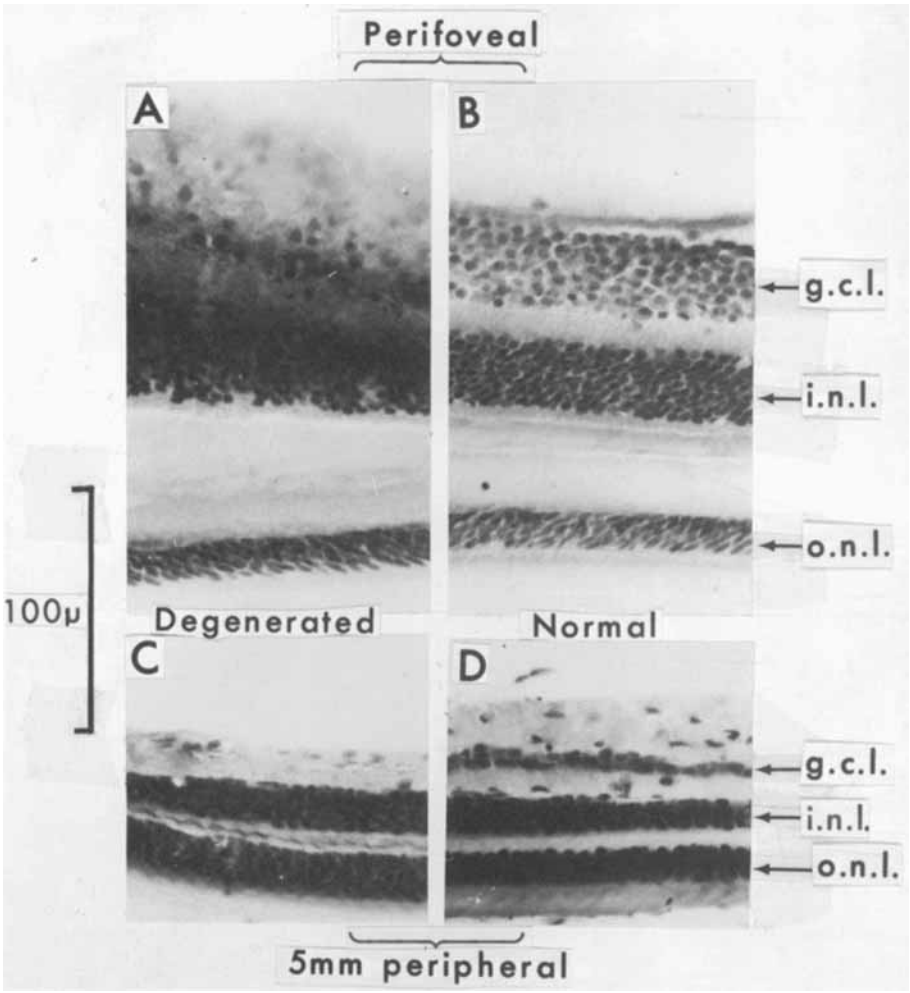


Fig. 12: Sections of the retina shown in figure 7A. A: Temporal margin of the foveola; B: Nasal margin of the foveola; C: Retina 5 mm temporal to the fovea; D: Retina 5 mm nasal to the fovea; g.c.l.: ganglion cell layer; i.n.l.: inner nuclear layer; o.n.l.: outer nuclear layer.

attempt to account for macular sparing in terms of the nasotemporal overlap of retina. For instance, Williams and Gassel ('62) describe two broad types of macular sparing, "true" and "false." In true macular sparing, vision appears to be maintained in the macular area of a hemifield rendered otherwise blind by a brain lesion, usually in or including visual cortex. They noted, however, that the spared central area may be 3–4° wide, much wider than the strip of overlap, and that in all the patients they examined some other part of the hemifield also retained function. They also noted that macular sparing could be induced, or abolished, by varying the technique of perimetry. They concluded that the occurrence of true macular sparing depends on the extent of the lesion, the attention of the subject and the technique of perimetry applied. False macular sparing was the term applied by Williams and Gassell to apparent survival of visual function in a 3–4° wide strip of an otherwise blind hemifield located adjacent to the vertical meridian of the visual field. These

workers report that survival of vision within the strip was always clearly attributable to eccentric fixation. Thus macular sparing as currently understood, does not seem to be clearly related to the approximately 1° wide bilaterally-projecting strip of retina described in this study.

The central projection of temporal retina

In the context of an analysis of the naso-temporal division of the cat's retina (Stone, '66) evidence was presented that ganglion cells in the area of retina temporal to the area centralis project to both ipsi- and contralateral optic tracts, and the suggestion was made that the axons of these contralaterally-projecting cells terminate in midbrain visual centres. The presence of contralaterally projecting cells in temporal retina of the cat has been confirmed (Laties and Sprague, '66; Ogawa et al., '69; Fukada, '71; Sanderson and Sherman, '71), and their projection to the midbrain has been demonstrated (Laties and Sprague, '66; Hoffmann, '69). Sanderson and Sherman ('71) have however presented evidence that some of these cells project to the thalamus, specifically to the medial interlaminar nucleus and to layer B of the lateral geniculate nucleus.

Contralaterally-projecting ganglion cells appear to be present in the temporal retina of other non-primate mammals. For example in both the grey squirrel and the tree shrew temporal retina projects to the contralateral superior colliculus (Lane et al., '71a). Evidence presented in this report suggests that such cells are not present in the monkey; i.e. all the ganglion cells located temporal to the strip of overlap appear to project to the ipsilateral optic tract. This is in accord with Lane et al.'s ('71b) evidence that in the owl monkey (in contrast to the grey squirrel and tree shrew) the superior colliculus does not receive fibres from ganglion cells in the temporal area of the contralateral retina. It may prove to be the case that an exclusively ipsilateral projection of temporal retina is to be found only in primates.

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