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ALTERED RETINOTECTAL TOPOGRAPHY IN HAMSTERS WITH NEONATAL TECTAL SLITS

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Abstract—Alterations in normal retinotectal topography by mechanical disruption of fiber passage during development was studied in Syrian hamsters using both neuroanatomical and electrophysiological techniques. The mechanical block to fiber passage was created with a medial to lateral slit across the superior colliculus on the day of birth. At maturity, topographically aberrant projections were found in areas of residual scar tissue. These aberrant projections were synaptically functional, producing neurons with mutiple, spatially separated visual receptive fields.

No evidence was found for an orderly compression of the retinotopic map in the tectum consequent to the transitory blockage of fiber passage.

THE RULES and conditions for the establishment of topographically organized projections have been investigated extensively in animals with regenerative nervous systems (see reviews by GAZE, 1974; MEYER & SPERRY, 1976; KEATING & KENNARD, 1976). Recently this investigation has been extended to the developing mammalian brain (SCHNEIDER, 1973; SCHNEIDER & JHAVERI, 1974; MILLER & LUND, 1975; CUNNINGHAM & SPEAS, 1975; FINLAY, 1976; FINLAY, WILSON & SCHNEIDER, 1979). Little is yet known about the limits and implications of modifiability of projection patterns in the mammalian brain. Particularly relevant to the mammalian brain is the role of function in the development of ordered projections, both at the level of synaptic efficacy and behavioral adaptiveness.

It has been shown both in animals with regenerative systems and in mammals that the retinotectal projection can be compressed into smaller than normal tectal areas (GAZE & SHARMA, 1970; JHAVERI & SCHNEIDER, 1974; UDIN, 1977; FINLAY, 1976). YOON (1972) has demonstrated that in goldfish the functional isolation of a portion of tectal tissue from other tectal tissue by a gel barrier is sufficient to induce a compressed retinotopic map in the isolated area.

In fetal rats, if a slit is made across the tectum, transiently interrupting tectal continuity and fiber passage, at maturity anomalous termination of fibers that would normally go to the caudal tectum are found in the neighborhood of the slit (MILLER & LUND, 1975). Three types of retinotopic organization are consistent with this observation: (1) two overlaid topographic maps of the retina are formed in the damaged colliculus, a compressed map rostral to the slit, and a normal map extended over the entire colliculus; (2) two orderly compressed maps are formed, one rostral and one caudal to the slit; and (3) one normal retinotopic map extends over the entire colliculus, with anomalous terminations only in the area of the slit. The type of pattern observed could provide insight into the mechanism by which orderly topographies are generated. To investigate this problem, we made mediolateral slits in the superior colliculi of newborn hamsters, and when the animals reached adulthood, we studied the topographic organization of the retinal projection using both neuroanatomical and electrophysiological methods. We examined in detail the topographies of the altered projections to determine which of the possible retinotopic maps were present. Comparison of the maps obtained by electrophysiological and neuroanatomical methods would indicate whether the aberrant projections have formed functional synapses.

EXPERIMENTAL PROCEDURES

Neonatal surgery

Within 24 h of birth, mediolateral collicular slits were made in hamster pups by the following procedure. A small incision was made in the scalp and the skin retracted so as to reveal the confluence of the transverse and superior sagittal sinuses, visible with the aid of a dissecting microscope. These features provide a guide to the rostral and lateral borders of the superior colliculi which are not yet covered by the cortex as they are in the adult. A small slit was made in the cartilaginous skull overlying the right colliculus and a fine scalpel was inserted and drawn from the midline to the lateral collicular border. The depth of cut was approx. 0.5 mm. The skin wound was then closed with sutures. This procedure was done under semi-sterile

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conditions; anesthesia was produced by mild hypothermia. After surgery, the animals were warmed and returned to the mother.

Neuroanatomical methods

When the animals were 6 weeks old, the distribution of the retinal projections to the right caudal superior colliculus was studied. The animals were anesthetized with a chlorohydrate/pentobarbitol mixture, 0.35 ml/100 g (Equi-Thesin, Jensen-Salsbery Laboratories) and small left nasal retinal lesions were made in five animals with an electrode using radiofrequency current. One day after eye surgery, 30 μCi of an equal mixture of [^{3}H]proline and [^{3}H]leucine were injected under anesthesia into the left eye via the lesion-hole so that no extra damage was caused to the retina. After an additional survival time of 24 h, the animal was perfused with saline followed by 10% formol-saline. Frontal sections of the brain were cut frozen at 30 μm thickness. One series of sections was stained by the Fink–Heimer procedure (FINK & HEIMER, 1967) and an adjacent series was processed for autoradiography (COWAN, GOTTLIEB, HENDRICKSON, PRICE & WOOLSEY, 1972). The L-[^{3}H]proline and L-[^{3}H]leucine were obtained from New England Nuclear Corporation.

Electrophysiological techniques

Details of the electrophysiological techniques have been described in a previous paper (FINLAY, SCHNEPS, WILSON & SCHNEIDER, 1978). Animals were anesthetized for recording with urethane (0.7 g/ml, 0.3 ml/100 g body weight) mixed with prednisolone (Depo-Medrol, 4 mg/ml, 0.2 ml/100 g body weight). The cranium overlying the colliculi was removed, the sagittal sinus ligated, cut and retracted, and the overlying cortex, including all visual cortical areas, was aspirated to give a full view of the neonatally slit colliculus and eliminate major non-retinal sources of visual innervation of the colliculus.

Axes of the visual field were defined by the following technique, used in prior neuroanatomical and neurophysiological experiments (FROST & SCHNEIDER, 1979; FINLAY, SCHNEB, WILSON & SCHNEIDER, 1978). Two small marks were made on the corneal margins at the midpoints of the attachments of the lateral and medial rectus muscles. These marks defined a nasotemporal meridian, and served as a necessary control for rotation of the eye. The optic disc was used as an intraocular landmark. The optic disc and the marked rectus insertions were aligned on the crosshairs of a reversible ophthalmoscope, and were projected onto a translucent hemisphere centered about the hamster's eye. The eye was held in position with sutures, protected by a contact lens of zero refractive power, and the pupil was dilated with a dilute solution of atropine. A 3–8° white spot, back projected onto the hemisphere, was the principal visual stimulus used.

Electrode penetrations were made approximately perpendicular to the surface of the colliculus, with the skull inclined 30°, nose up, from the normal stereotaxic horizontal. Single unit potentials were recorded with glass-coated platinum–iridium microelectrodes 1–2 μm in diameter at the tip; in normal tissue, almost all of the single and multiunit responses recorded by these electrodes were shown in a previous study to be generated from postsynaptic tectal units (FINLAY *et al.*, 1978). Both single and multiunit responses were used to assess retinotectal topography. In collicular areas where multiple, spatially separate receptive fields were found for multiunit evoked responses, an effort was made to isolate single neurons. Single units were isolated by differential amplitude by a voltage discriminator and waveforms were superimposed, to verify both waveform and amplitude identity. A unit thus isolated with a dual, spatially separated receptive field was considered a presumptive postsynaptic tectal unit. Nine such units were isolated.

For all single and multiunit responses receptive field size, presence of spatially separated visual fields, definition of receptive field boundaries and spontaneous activity were assessed. Small lesions to allow subsequent histological reconstruction of electrode penetrations were made at the end of each recording session.

RESULTS

Neuroanatomical experiments

The topography of the retinotectal projection was studied in five animals with tectal slits on the day of birth, using a combined Fink–Heimer degeneration and autoradiography technique. One of the animals showed excessive tectal damage and data from it are not reported here. In the remaining animals, healing of the tectal slit was considerable. In three, scar tissue extended through only part of the mediolateral extent of the superior colliculus, while the fourth showed no residual scar tissue. In all four animals, the operated superior colliculus was somewhat smaller than normal (Fig. 1).

These four animals received small nasal retinal lesions, in addition to autoradiographic labeling of the same eye. The three animals of this group having residual scar tissue showed very similar patterns of degeneration. In addition to a focus of degeneration at the caudal pole of the superior colliculus as expected from a nasal retinal lesion, an aberrant projection was located close to the scar. This is indicated in a dorsal view reconstruction of one of the animals (Fig. 1). The aberrant degeneration found at the site of the scar was quite dense (Fig. 2B). In the lateral geniculate nucleus of these animals, degeneration was found only at the appropriate area.

These three animals showed one further abnormality. In normal adult animals, if a small lesion is placed in the retina, and the eye is injected with labeled amino acids 1–4 days later, the degenerating terminals are found in a discrete area of the superior colliculus occupying the whole depth of the superficial gray layer, and the radioactivity in the corresponding area of the superior colliculus is very low and not distinguishable from the background level (unpublished observations). However, the aberrant projections in the region of scar tissue resulting from the tectal slit did not occupy the whole depth of the superficial gray layer. In two cases, they were found in the deep part of the superficial gray layer (Fig. 2A and B), while in the third animal these aberrant projections, as indicated by the degeneration, were found in the superficial part of the superficial gray layer instead. In addition to this abnormal distribution in depth, in all three animals there was also

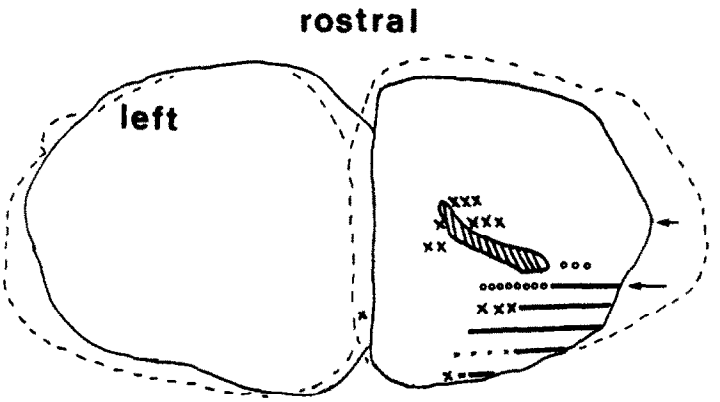


FIG. 1. Dorsal view reconstruction of the superior colliculus from Fink–Heimer stained sections of an animal with a mediolateral slit in the right superior colliculus on the day of birth. A left nasal retinal lesion was performed and the left eye was injected with labeled amino acids when the animal reached adulthood. Solid lines indicate the size of the superior colliculus in this hamster: the dashed line indicates the normal size. Other symbols: ///, scar tissue; ——, dense degeneration which spans the whole depth of the superficial gray layer of the superior colliculus; ·····, sparse degeneration which spans the depth of the superficial gray; OOO, degeneration which spans the superficial half of the superficial gray; × × ×, degeneration which is restricted to the deeper half of the superficial gray. Arrows indicate the rostro–caudal levels where photomicrographs were taken (Fig. 2). Note the aberrant projection around the scar tissue.

evidence of abnormal intermixing of fibers from disparate retinal areas. In some areas adjoining scar tissue, both the level of degenerating terminals and radioactivity was high (Fig. 2B and C), indicating that fibers from the lesioned nasal retina, and other, intact retinal areas, were both present.

In the caudal pole of the colliculus, where no scar tissue was present, a similar pattern could be seen. In two animals, in the caudal colliculus, fibers from neighboring retinal areas occupied different depths in the superficial gray layer (Fig. 2D, E and F). Vertically and horizontally overlapping regions of projection were also observed, suggesting that retinal fibers were distributing over a wider area than normal and intermixing to an unusual degree. This is never observed in normal animals.

Retinotectal topography as revealed by electrophysiological techniques

Eight animals were studied. Of these, one showed no abnormality in retinotectal topography, and two had excessive scar tissue and tectal tissue loss, and data from them were not interpretable. The remaining five showed evidence of abnormal retinotopic organization in the region of the neonatal tectal slit. Three types of abnormalities were observed: (1) single neurons with unusually large visual receptive fields; (2) single and multiunit topographically mislocated receptive fields; and (3) single neurons with multiple, spatially separated receptive fields. Neurons with abnormal receptive field extent or location were found in 9 out of 138 electrode penetrations in five animals. Later histology showed all nine penetrations to be located directly adjacent to or in an area of scar tissue.

An example of a colliculus in which all three types of abnormality were found appears in Fig. 3(A) and (B). Figure 3(A) shows those electrode penetrations and associated receptive fields that were as orderly as those found in a normal colliculus. Figure 3(B) shows the positions of the electrode penetrations associated with abnormal visual receptive fields later found by histological study to be located in an area of scar tissue.

In addition, all five animals showed a reduction of the total amount of superficial gray tissue. The amount of remaining superficial gray was assessed in three ways in these animals: (1) rostral to caudal length of the colliculus at the point of maximum extent, from a dorsal view of the superior colliculus perpendicular to the collicular surface (i.e. measured in the plane perpendicular to the electrode penetrations); (2) surface area, measured from the same dorsal view; and (3) volume. Volume was estimated by determining the area of the smallest rectangle that would include the medial, lateral, dorsal and ventral extent of the superficial gray for each section taken perpendicular to the dorsal collicular surface. Sections were separated by 150 μm, and this was multiplied by each area measurement and then summed to give a volume estimate for the entire colliculus. The five animals showed an average 16% (range 27–10%) reduction in rostral to caudal length, 28% (range 44–6%) reduction in collicular surface area, and a 29% (range 37–23%) reduction in estimated volume.

In the animal shown in Fig. 3, the colliculus is 17% less than normal in rostral to caudal length, and 41% in surface area. Considering both the normal and abnormal receptive fields recorded for this animal, however, it is clear that nearly the entire visual field represented in a normal colliculus (70° nasal to the optic disc and 90° temporal to the optic disc) is repre-

FIG. 2. Same case as in Fig. 1. All drawings and photomicrographs are from cross-sections.

(A) Outline of the superior colliculus from a Fink–Heimer section (rostral to caudal level: see the short arrow in Fig. 1). Dots: degenerating terminals; parallel lines: scar. The solid rectangle outlines the area where the degeneration was found to be most dense; a high-power photomicrograph of it is shown in Fig. 2(B). The dashed rectangle outlines the area of the photomicrograph taken from an adjacent autoradiographic section (Fig. 2C).

(B) Dark-field Fink–Heimer photomicrograph of the aberrant projections situated next to the scar tissue (*). Scale: 100 μm.

(C) Dark-field photomicrograph of an autoradiographic section adjacent to the Fink–Heimer section shown in Fig. 2(A). The broken lines outline the location of degeneration as indicated from an adjacent Fink–Heimer section. Also see Fig. 2(A); star (*): scar tissue. The black arrow points to the area where fibers from disparate retinal areas were intermixing. Scale: 100 μm.

(D) Outline of the superior colliculus from a Fink–Heimer section (rostro–caudal level: see the long arrow in Fig. 1). Dots: degenerating terminals.

(E) Outline of the superior colliculus from an autoradiographic section which is adjacent to the section shown in Fig. 2(D). Dots: radioactivity indicating locations of retinal projections. The dashed rectangle outlines the area where a photomicrograph was taken (Fig. 2F).

(F) Dark-field photomicrograph of the same section as in Fig. 2(E). Same magnification as Fig. 2(C).

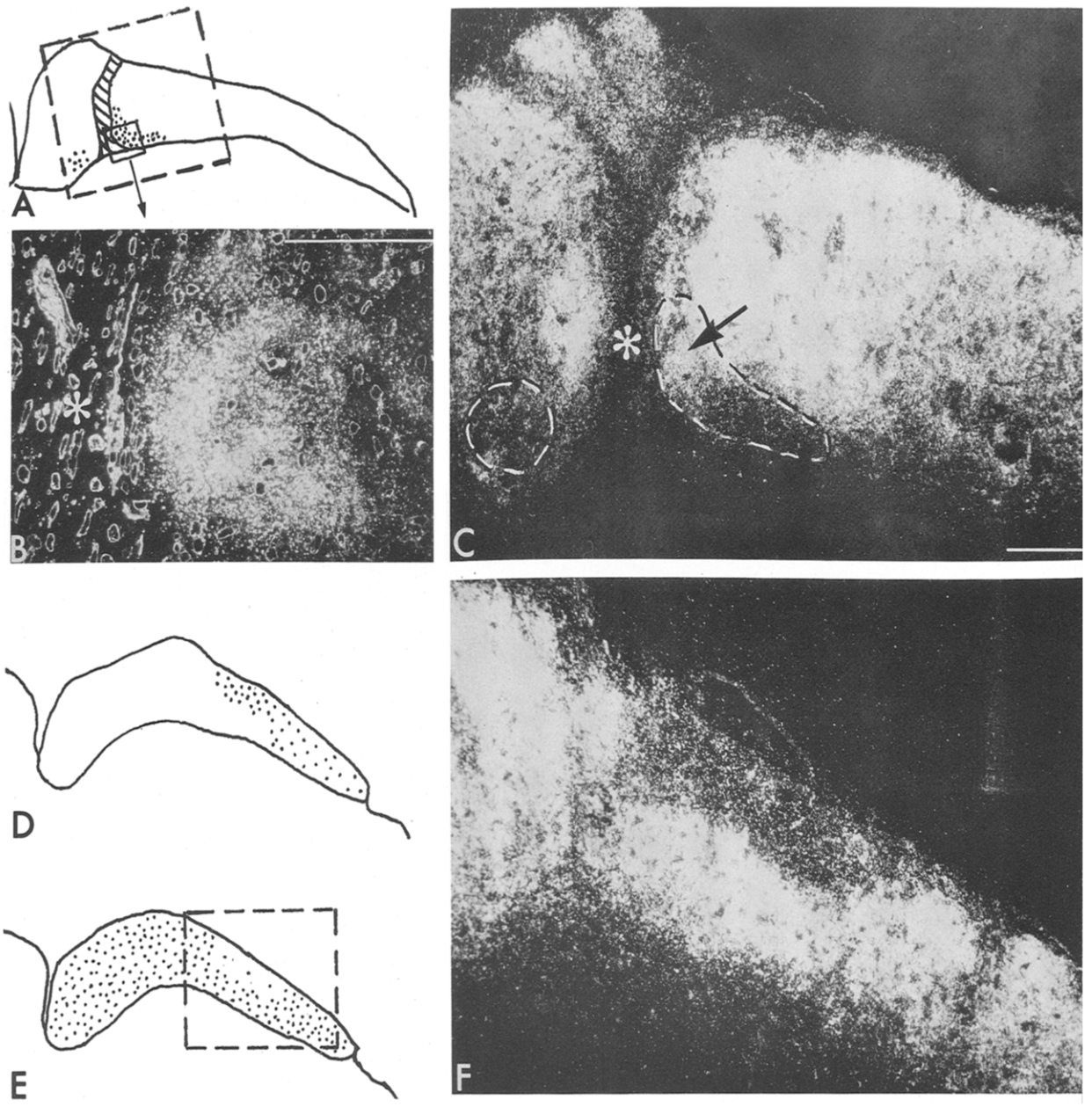
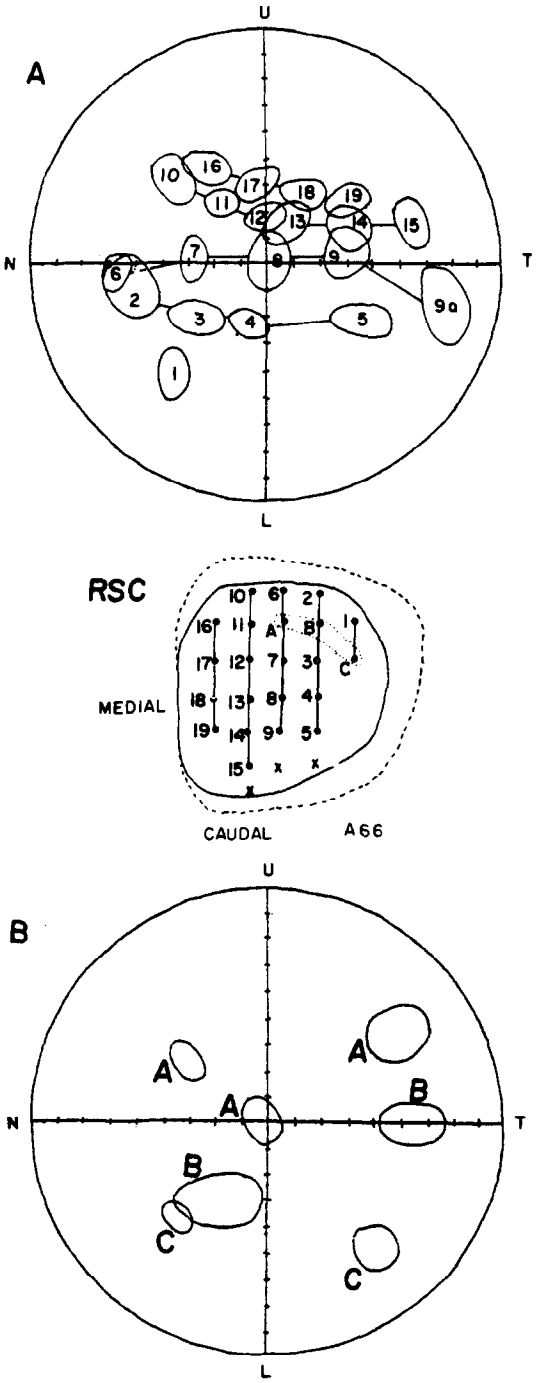


FIG. 2.

sented in this colliculus with the exception of 10–15° of the most temporal visual field. The pattern of peripheral field loss and compression of the remainder of the visual field into a smaller than normal collicular area conformed to the pattern observed in a previous study of reorganization of collicular topography after partial collicular lesions (FINLAY, 1976). In the caudalmost colliculus, the representation of the most temporal visual field was often found deep to the collicular surface (as in penetration 9, Fig. 3A). The remaining four animals showed a similar pattern.



Assuming most tissue loss would have occurred in areas adjacent to the scar, it is interesting to observe that no animal showed an obvious gap in the central visual field corresponding to the scar location. This was verified semiquantitatively in the following manner: for each animal the rostro–caudal extent of the superior colliculus that bisected the neonatal slit was measured from the dorsal view reconstruction. Comparing this to the corresponding length from a normal colliculus, the amount of tissue loss was determined. Taking the last electrode penetration with a visual receptive field rostral to the scar as a starting point for estimation and using available data about the projection of the visual field onto the surface of a normal colliculus (FINLAY *et al.*, 1978), we determined the scotoma that would be expected in the central visual field for a tissue loss of the magnitude calibrated in each animal. We then determined if the area of expected scotoma was represented in each animal. In each case, it was. For example, in Fig. 3, for penetrations 2–5, a scotoma of approximately 25° extending from receptive field 2 along the nasotemporal meridian would be expected for the amount of tissue loss in this animal. Even considering only topographically normal receptive fields (Fig. 3A), it is apparent that no scotoma of this magnitude exists.

Neurons located near areas of scar tissue had receptive fields which clearly deviated from the normal topographic representation of the retina in several respects, yet retained some evidence of normal order. The most striking deviation from the normal order was the presence of multiple, spatially separated receptive fields for single neurons (penetrations A, B and C, Fig. 3B). The relative efficacies of the separated

FIG. 3. Position of electrode penetrations in neonatally slit right superior colliculus and corresponding contralateral visual receptive fields. The superior colliculus is shown in dorsal view in the plane used for electrophysiology. The unbroken line shows the appearance of the superior colliculus in this hamster; the broken line represents the normal appearance of the colliculus. The dotted line encloses the area where scar tissue was found. Open circles and digits indicate penetrations where normal visual receptive fields were found; these receptive fields are shown in visual field diagram A. Lines link rostral to caudal series of penetrations in the colliculus and corresponding lines link associated visual receptive fields.

Closed circles marked with letters indicate abnormal visual receptive fields; these are shown in diagram B. X indicates sites of collicular penetrations where no visual response was found; these penetrations touched only the cell-sparse caudal margin of the colliculus and do not indicate unresponsive superficial gray cells.

The nasal (N) to temporal (T) axis of the visual field is defined by the line connecting the midpoints of the attachments of the lateral and medial rectal muscles, and the upper (U) to lower (L) axis is defined by the attachments of the superior and inferior rectus muscles. The field is centered about the optic disc. RSC, right superior colliculus.

fields in producing a reliable postsynaptic response varied with the depth of the electrode in the colliculus in an unpredictable way. For example, for penetration A, the most temporal and the most nasal fields were recorded simultaneously from single neurons in the uppermost superficial gray. As the electrode was lowered, subsequently recorded cells had similar nasal fields, but lacked temporal fields. In the deepest part of the superficial gray, the middle visual field shown in Fig. 3B appeared.

Two facets of the normal topographic representation were preserved. First, the approximate order on the upper to lower visual axis (mediolateral collicular axis) was maintained (Fig. 4). Second, no abnormal fields were found whose locations were more nasal than would have been predicted from the surrounding penetrations associated with normal topographic representation. In general, the locations of abnormally large or mislocated visual receptive fields corresponded roughly to those that would be expected to occur caudal to the recording site in this animal and all other animals (Fig. 4).

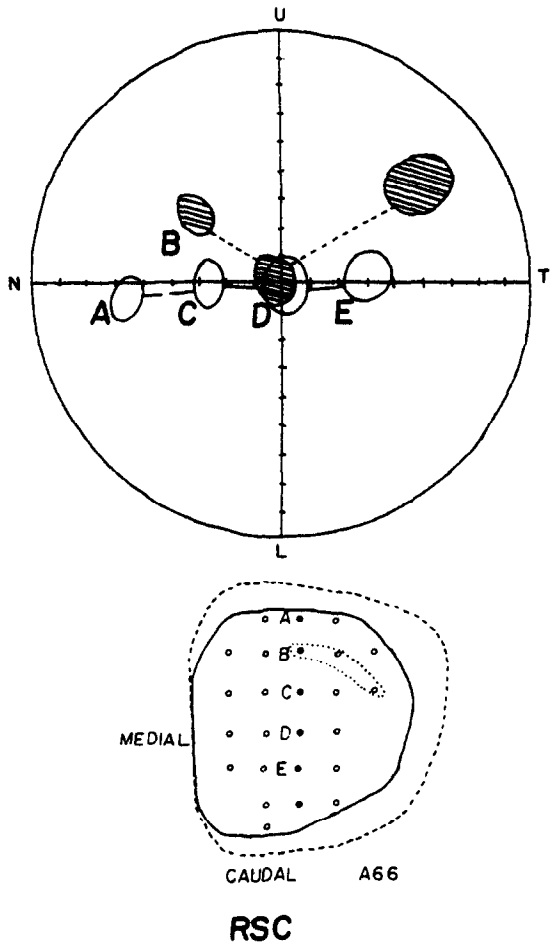


FIG. 4. Normal and abnormal receptive fields associated with a single rostral to caudal series of penetrations for the hamster shown in Fig. 3. Penetration B was associated with multiple visual receptive fields, which are hatched in the diagram. RSC, right superior colliculus.

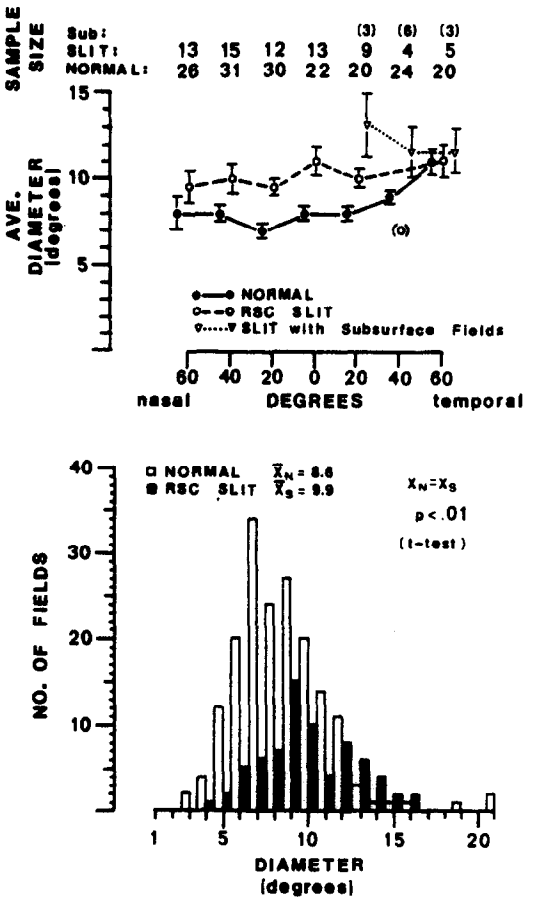


FIG. 5. Top: Average size of visual receptive fields recorded at various receptive field locations along the nasotemporal meridian in normal superior colliculus (solid lines) and neonatally slit colliculi (dashed lines). Error bars indicate one standard error of the mean. Bottom: Distribution of receptive field sizes over all receptive field locations for normal and neonatally slit colliculi. RSC, right superior colliculus.

Receptive fields of neurons in the damaged colliculi

Both quantitative and qualitative methods were used to assess receptive field size and organization of neurons in neonatally slit colliculi. Receptive field size was assessed quantitatively. Receptive field size was taken as the average of the angular extent of the major and minor axis of the activating region of the receptive field. In Fig. 5, the average receptive field size at different positions along the nasotemporal axis is plotted for both normal superior colliculi, and the neonatally slit colliculi. Receptive fields of units from neonatally slit colliculi overall (bottom figure) and for subsectors of the visual field (top figure) were consistently and significantly larger than normal. Fewer data points for the diameter of the receptive fields of units from slit colliculi were available for the temporal visual field, since this area was often not represented on the collicular surface, but only deep to the surface. The sizes of the available subsurface fields (top figure) have been indicated; these, however, even in normal animals, are typically larger

than surface fields (FINLAY *et al.*, 1978; TIAO & BLAKEMORE, 1976; CHALUPA & RHOADES, 1977).

Normal collicular units have the following combination of response properties: brisk, transient and non-habituating activation by small moving or flashed stimuli; well-defined receptive field boundaries; low spontaneous activity; and poor response to full-field illumination (FINLAY *et al.*, 1978; TIAO & BLAKEMORE, 1976; CHALUPA & RHOADES, 1977). The great majority of units in the damaged superior colliculi, including those with dual receptive fields, were not noticeably abnormal on any of the above criteria. Some of the abnormal units, particularly those with the largest receptive fields, were abnormal by one or several of the above criteria, showing high rates of spontaneous activity, or habituating with repeated stimulation. In two cases, the definition of receptive field boundaries was so poor that the location of the receptive field could only be assigned to a quadrant with certainty.

DISCUSSION

The neuroanatomical and electrophysiological results obtained in different animals are in close agreement, showing similar patterns of anomalous termination in the neonatally slit colliculi. Both results show evidence of two distinct alterations of retinotectal topography.

First, the anatomical results indicated that aberrant projections were formed in the area of the neonatal slit, and that topographically appropriate and inappropriate retinal projections showed significant amounts of overlap in these areas. This correlates directly with the physiological finding of multiple, spatially separate receptive fields for single and multiunit groups of neurons located near areas of scar tissue. Other sources of visual input, thalamic, pretectal and nigral, may also contribute to the electrophysiologically evoked response. Neither the anatomical nor the electrophysiological methods showed any evidence for dense aberrant projections to any tectal area not immediately adjoining scar tissue.

Second, anatomical results showed that all the neonatally slit colliculi were reduced in size, and that fiber populations from separate retinal areas were failing to segregate as clearly as normally in the caudal colliculus. This finding correlates directly with the physiological finding of compression in the representation of the visual field into a smaller than normal collicular area, with a corresponding increase in the size of the receptive field for single neurons. The most plausible explanation for both results is that retinal ganglion cells representing a larger retinal area than normal are converging onto single tectal cells.

Recent research on the normal development of the hamster retinotectal projection sheds some light on the probable sequence of events following neonatal surgery. On the day of birth, very few retinal fibers have occupied the superior colliculus (SO, SCHNEIDER & FROST, 1978). Thus, a tectal slit performed on the day of birth would have damaged few growing retinal fibers. Since evidence of scar tissue was restricted in mediolateral extent, while the original slit extended across the entire medial to lateral extent of the superior colliculus, healing of the damaged area was considerable. It is thus likely that most retinal fibers were only transiently blocked in their normal rostral to caudal progression across the colliculus. In the hamster, there is a limited period extending to 2 weeks post natal in which major rearrangements of retinotectal fibers under the conditions of this experiment are possible (SO & SCHNEIDER, 1978). In those tectal areas where healing was not complete within this period, axons may have been prevented from passing and their anomalous termination pattern persisted to maturity.

Our findings support and extend the findings of MILLER & LUND (1975) in rats. We have confirmed the finding of anomalous projections to areas of early tectal damage; we also show that the anatomical and physiologically measured retinotopic maps in the tectum are quite similar, strong evidence that these aberrant connections are physiologically functional. We find no evidence for a compressed retinotopic map rostral to the mediolateral slit, though we cannot rule out the possibility that such a map may have been formed transiently during development. The only aberrant projections found were located directly in areas of scar tissue. Although these areas may have been in some way functionally isolated by the scarring process, limiting the normal process of fiber interaction, we can show no evidence for induced reorganization in the pattern of retinal terminations in normal tectal areas adjacent to damaged tectal areas with abnormal termination patterns.

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