

# Anomalous Ipsilateral Retinotectal Projections in Syrian Hamsters with Early Lesions: Topography and Functional Capacity

BARBARA L. FINLAY,<sup>1</sup> KAREN G. WILSON<sup>2</sup> AND GERALD E. SCHNEIDER  
*Department of Psychology, Massachusetts Institute of Technology,  
Cambridge, Massachusetts 02139*

**ABSTRACT** Retinotectal topography, response properties of neurons in superior colliculus, and visual orienting behavior were studied in hamsters whose superior colliculi were innervated by one or the other of two types of anomalous ipsilateral projections.

For the first type, an abnormally large uncrossed projection was created by monocular enucleation on the day of birth. This projection extended over the superficial part of the rostral half of the colliculus. The upper visual field was represented medially, and the lower visual field laterally, which corresponds to a normal projection. The rostrocaudal axis was disordered, but showed a slight tendency for nasal visual field to be represented rostrally and temporal field caudally; this tendency corresponds to an inversion of the normal ipsilateral projection, fitting instead the pattern of a contralateral projection.

For the second type of anomalous ipsilateral projection, an abnormal intertectal decussation of optic tract fibers was created by neonatal ablation of the superficial layers of one superior colliculus and removal of the ipsilateral eye (Schneider, '73). Retinotectal topography observed in this recrossing projection was predominantly mirror-symmetric to the normal contralateral projection; however, some distortions in retinotopic order were observed, including misplaced fields and local inversions of the mirror-symmetric topography, and distortions of local magnification factor. Response properties of single units found medially in the left colliculus were similar to those found in normal colliculus. Units found more laterally were underresponsive, showing response decrements with repeated stimulation which is abnormal for units in the superficial gray, and many had abnormally large receptive fields. This physiological pattern was reflected in the pattern of errors made in visual orienting to small targets.

It was concluded that polarity cues exist in the tectum sufficient to order the terminals of the retinotectal projection independent of the direction of fiber arrival or order in the optic tract as it enters the tectum. In addition, the functional competence of the abnormal recrossing retinotectal projection has been demonstrated by both electrophysiological and behavioral methods.

The ipsilateral projection of the retina in mammals normally originates in the area of temporal retina where the fields of vision of the two eyes overlap. Thus, in mammals with laterally placed eyes, the ipsilateral projection is considerably smaller than the contralateral projection. Neuroanatomical studies in mammals have shown that the small ipsilateral projection to the superior colliculus

may show a considerable increase after either of two types of early lesions: monocular enucleation, or unilateral tectal ablation.

In rat (Lund et al., '73; Lund and Miller, '75), after fetal or neonatal eye removal on one

<sup>1</sup> Present address: Department of Psychology, Uris Hall, Cornell University, Ithaca, New York 14853.

<sup>2</sup> Present address: Department of Entomology, North Carolina State University, Raleigh, North Carolina 27607.

side or after a monocular partial retinal lesion (Lund and Lund, '76), the ipsilateral projection from the other eye to the superior colliculus shows an increased distribution, including the entire extent of the denervated ipsilateral colliculus. This increase is due, at least in part, to branching of contralaterally going fibers at the optic chiasm (Cunningham, '76). Some residual increase in quantity and granule size of terminal degeneration, attributed to sprouting of the existing projection, appears to occur after monocular enucleation in mature rats as well (Goodman et al., '73). In hamster (Frost and Schneider, '76, Schneider, '73), neonatal monocular enucleation also causes an increase in area and laminar distribution in ipsilateral collicular innervation, though not as extensive as reported for the rat. In rabbit (Chow et al., '73), an increase in ipsilateral retino-tectal axons after early monocular enucleation has also been observed, though it is smaller still.

In hamsters, contralaterally going retinofugal fibers can also be induced to recross the midline at the level of the colliculus to innervate the intact ipsilateral colliculus by a neonatal unilateral tectal lesion (Schneider, '73; fig. 4, this study). This ipsilateral projection is much heavier than the ipsilateral projection produced by monocular enucleation. Such an effect can also be demonstrated in rats (Miller and Lund, '75). If both eyes remain after a unilateral tectal ablation, the recrossing projection is usually confined to the medial bank of the ipsilateral colliculus (Schneider, '73), and the remainder of the superficial gray layer is innervated by its normal input from the contralateral eye. If the eye contralateral to the remaining colliculus is removed at birth, the recrossing projection will spread over the entire extent of the ipsilateral colliculus (Schneider, '73).

The retinotopic organization of these anomalous ipsilateral projections is interesting not only because of its functional significance, but also with regard to theories of the normal development of orderly topographic projections. In animals with the capacity for central nervous system regeneration, the retinotectal system has been investigated extensively since the pioneering work of Sperry ('44) (see reviews by Gaze, '70; Meyer and Sperry, '76; Keating, '76). In particular, creation of anomalous ipsilateral projections by uncrossing the optic nerve in animals in which the optic

nerve can regenerate was one of the first tests of the specificity of retinotectal connectivity (Sperry, '45).

Experiments in mammals extend this general paradigm and introduce some new factors involved in the development of retinotectal topography. Lund and Miller ('75) report that in rat the topography of the anomalous ipsilateral projection created by monocular enucleation is predominantly mirror-symmetric to the normal contralateral projection, according to experiments using anatomical degeneration techniques. Cunningham and Speas ('75), however, report a paradoxical organization, consisting of two overlaid topographies with opposite order along the mediolateral axis, representing the dorsoventral axis of the retina. In hamster, after unilateral eye enucleation and homolateral tectal ablation at birth, initial experiments showing patterns of degeneration in the remaining colliculus after small retinal lesions in the adult were not encouraging in indicating an orderly topography (Schneider and Jhaveri, '74); while a mirror-symmetric focus of terminal degeneration could usually be identified, other scattered patches of non-mirror-symmetric terminal debris were also present.

The functional capacity, both physiological and behavioral, of anomalous optic-tract connections resulting from lesions in young mammals has not yet been completely described for any one animal. In rat, the anomalous ipsilateral projection created by monocular enucleation both exhibits normal-appearing synapses (Lund et al., '73; Lund and Miller, '75), and can activate post-synaptic units (Cunningham and Speas, '75). In rabbit, the anomalous ipsilateral projection does not appear to be sufficient to drive post-synaptic units (Chow et al., '73). In hamster there is behavioral evidence for misdirected visual orienting due to anomalous connections (Schneider, '73, '77; Schneider and Jhaveri, '74).

This study was undertaken to examine, using electrophysiological techniques, the retinotectal topography of anomalous ipsilateral projections in the hamster: both the increased projection created by monocular enucleation alone, and the recrossing projection created by monocular enucleation combined with a unilateral tectal lesion. The response properties of single neurons in these altered colliculi were investigated to determine the functional capabilities of the abnormal ipsilateral projec-

tions. Finally, the relationship of the three techniques that have been used to assess retinotectal topography, i.e., neuroanatomical tracing, electrophysiology, and analysis of visually elicited turning responses, was assessed by using combinations of these techniques on single animals.

#### METHODS

Seventeen Syrian hamsters (*Mesocricetus auratus* Waterhouse), of both sexes and at least three months old, were used for electrophysiological recording. Visual orienting behavior has been studied in an additional 22 hamsters.

##### *Neonatal surgery*

Within 24 hours of birth, hamster pups were subjected to one of two surgical procedures. Mild hypothermia provided anesthesia. For the first group (5 animals), one eye was removed, with the aid of a dissecting microscope, by making a small slit under the line of the prospective eyelid and withdrawing the eye with fine forceps, with care to remove all pigmented fragments of the eyeball. For the second group (12 animals), monocular enucleation was coupled with ipsilateral tectal ablation. A small incision was made in the scalp, and the skin retracted so as to reveal the confluence of the transverse and sagittal sinuses, visible through the cartilagenous cranium, and the occipito-interparietal suture. These features define the extent of the superior colliculus, which is not yet covered by cortex as it is in the adult. The superficial gray layer of the superior colliculus was destroyed unilaterally by application of heat to the unopened skull. The extent of each lesion was determined in the adult brain by histology. After the lesion had been made, the skin wound was closed with sutures and the animal was returned to the mother.

##### *Adult surgery and electrophysiological recording*

Details of anesthesia, surgery, optics and visual stimulation have been described in a previous paper (Finlay et al., '78). Animals to be used for electrophysiology were anesthetized with urethane (0.7 g/ml, 0.3 ml per 100 g body weight) mixed with prednisolone (Depo-Medrol, 4 mg/ml, 0.2 ml per 100 g body weight), a corticosteroid used to reduce inflammation and cerebral edema. The cra-

nium overlying the colliculi was removed, the sagittal sinus ligated, cut and retracted, and overlying cortex, including all visual cortical areas, was aspirated to give a full view of the colliculi and eliminate non-retinal sources of visual innervation of the colliculus. Since removal of cortex does alter some of the visual response properties of cells in the superior colliculus, in particular direction selectivity (Chalupa and Rhoades, '77), we are thus assessing the relative normality of the constellation of response properties produced by the more direct visual input from the retina.

Axes of the visual field were defined by the following technique, used in prior neuroanatomical and neurophysiological experiments (Frost and Schneider, '79; Finlay et al., '78; Jhaveri and Schneider, '74). Two small marks were made on the corneal margins at the mid-points of the attachments of the lateral and medial rectus muscles. These marks defined a nasotemporal meridian (*not* the same as "true" horizontal as defined with respect to the floor in an awake animal) and served as a necessary control for eye rotation. The optic disc was used as an intraocular landmark; it was located with a reversible ophthalmoscope and its projection was plotted on a translucent hemisphere centered about the hamster's eye. The eye was sutured in place, 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 (Schneider, '69). Single-unit potentials were recorded with glass-coated platinum-iridium microelectrodes 1-2  $\mu\text{m}$  in diameter at the tip; almost all the single and multiunit responses recorded by these electrodes were shown in a previous study to be generated from postsynaptic tectal cells (Finlay et al., '78). Both single and multiunit responses were used to assess retinotectal topography. In addition, when single units were isolated, receptive field size, spontaneous activity, the sustained or transient character of the response, response decrements with repeated stimulation, contrast preference, and direction-of-movement preference were assessed. Small lesions to allow subsequent histological reconstruc-

tion of electrode penetrations were made at the end of each recording session.

### *Histology*

Hamsters were sacrificed immediately following recording and perfused with saline followed by 10% formol-saline. Coronal sections in the plane parallel to the angle of electrode penetration, 30° from the standard coronal plane, were cut at 30  $\mu$ m. One series of sections was stained with cresylecht violet; other series were stained using the Loyez method for myelin, or a silver-pyridine stain for normal fibers (Fink and Schneider: Schneider, '69) as required to determine the extent of reorganization consequent to the neonatal lesion. Brains were reconstructed with the aid of a standard dorsal-view reconstruction in the electrophysiology plane. In one animal that had received a small retinal lesion two days prior to recording, a series of sections was stained for anterograde degeneration using a modified Nauta technique (Fink and Heimer, '67).

Both autoradiography and electrophysiology were combined in one animal which had a monocular enucleation at birth. Twenty-four hours prior to recording, 30  $\mu$ Ci of  $^3$ H-leucine and  $^3$ H-proline, in equal amounts, were injected into the eye in a 1  $\mu$ l volume, the injecting needle entering nasally through the sclera near the limbus. Care was taken to prevent infection and to avoid detaching of the retina; in addition, the animal's contralateral superior colliculus was mapped completely to delineate any unresponsive areas in the visual field. After recording, the animal was perfused with 10% formol saline and prepared for autoradiography.

### *Analysis of visual orienting behavior*

For testing visually elicited turning, hamsters were pretrained to stand on a small elevated platform and hold their noses relatively motionless in a hole in a small upright panel. Rewards at this stage were sunflower seeds pushed through the hole. The visual stimulus was a small rubber sphere, 1.2 cm in diameter, which could be presented suddenly by moving it into the visual field from behind a baffle 14 cm from the hamster's head. The stimulus could be presented at various positions in the visual field. An overhead camera and a frontal camera videotaped the visually elicited orienting movement as well as the stimulus. Only orienting movements initiated within

two seconds of stimulus presentation were scored. The hamster was rewarded with the sunflower seed as rapidly as possible when he ceased his head movement, regardless of the accuracy of the turn. Stimulus position and initial direction of each head movement was determined by slow and stop-motion playback of the videotape. Because it is not possible to monitor the hamster's eye movements in these conditions, this perimetry procedure yields maps based only on head coordinates of positions of stimuli eliciting accurate and inaccurate turns. The hamster also has ample opportunity to make use of visual feedback during this turning movement (Schneider et al., '75).

## RESULTS

### *Neonatal removal of one eye*

The topography of the visual field represented in the ipsilateral retinal projection to the tectum was studied in five hamsters in which one eye had been removed on the day of birth. It is important to note at this point that (in our decorticate preparation) we were unable to record any units in the superior colliculus of normal adult hamsters which could be activated by visual stimulation of the ipsilateral eye (Finlay et al., '78). Therefore, we assume that most recordable activity of the ipsilateral retinotectal input in animals with one eye removed at birth was due to an augmentation of, or an addition to, the small normal pathway.

In the ipsilateral colliculi of animals in which one eye had been removed at birth, units sensitive to visual stimulation could be found over the entire medial-to-lateral extent of the rostral half of the colliculus. The ipsilateral projection in its general form was quite consistent in all five animals. An orderly topography along the mediolateral axis was observed, such that units activated by stimuli in the upper visual field were located in medial colliculus, and units activated by stimulation of the lower visual field were found in lateral colliculus. The entire upper to lower extent of visual field found in normal contralateral colliculus was found. The nasotemporal order of visual receptive fields recorded in penetrations along the rostro-caudal axis of the colliculus was quite disorderly. The entire visual field was not represented; the temporal retina is the major source of the enlarged ipsilateral projection. Of the 88 penetrations made in ipsilaterally innervated colliculi, units recorded

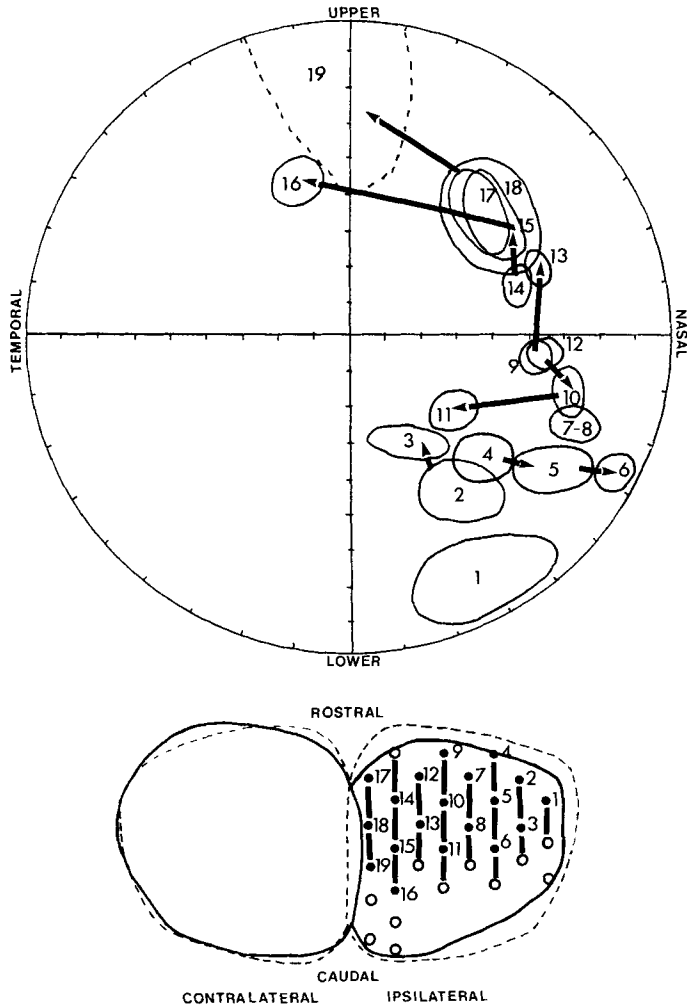


Fig. 1 Position of electrode penetrations in the right superior colliculus and corresponding ipsilateral visual receptive fields. The superior colliculi are shown in dorsal view in the plane used for electrophysiology. The broken line corresponds to the normal appearance of the colliculus; the solid line represents the reconstructed appearance of the colliculus in this hamster. Filled circles indicate penetrations where a visual receptive field could be located; open circles indicate areas of no response. Bars connect rostral to caudal series of penetrations. Corresponding bars connect receptive fields in the visual field diagram; the arrows indicate the rostral to caudal relationship of the corresponding penetrations in the colliculus. Dotted lines indicate receptive fields with indeterminate boundaries. The visual field map is marked off every  $10^\circ$  and is centered on the optic disc. The nasotemporal and upper-lower meridians are defined by the attachments of the extraocular muscles.

in 80 of them had receptive fields lying in the nasal  $70^\circ$  of visual field; only in eight did the fields lie principally in the temporal  $90^\circ$  of visual field. In only one penetration were units found with receptive fields lying within  $20^\circ$  of the temporalmost border of the visual field. An example of visual receptive fields and corresponding penetrations in the col-

liculus for one hamster, whose left eye had been removed at birth, is shown in figure 1. The shrinkage indicated for the ipsilateral colliculus is a normal result of neonatal eye enucleation.

Receptive field properties were in general similar to those observed in normally innervated contralateral colliculus (Chalupa and

Rhoades, '77; Finlay et al., '78; Tiao and Blakemore, '76), with some notable exceptions. Units responded to both moving and flashed stimuli in their receptive fields; stimuli could be either light or dark relative to the background. Units showed little or no spontaneous activity. No cells sensitive to the direction of stimulus movement were located; however, this population of units is small even in normal colliculus, and is sensitive to decortication.

Unlike the fields of normal cells in the contralateral colliculus, receptive fields were often quite large, ranging from 10° to 50° in diameter. (In normal animals for comparable nasal visual field, receptive fields average 14° in diameter with a range of 8-22°.) Particularly in the caudalmost part of the projection, receptive field borders were very ill-defined, and units often habituated with repetitive stimulation.

We were quite interested in any covert order that might appear in the rostrocaudal axis of the colliculus. Several observations suggested that there might be such an order. Most units had fairly discrete receptive fields along the naso-temporal axis; single receptive fields usually did not encompass the entire nasotemporal representation seen in a rostral to caudal series of penetrations, and units with receptive fields that were extremely elongate nasotemporally were never observed. There appeared to be patches of local order; both nasal to temporal and temporal to nasal progressions were observed over small rostral to caudal extents of the colliculus. No spatially separated visual fields were observed for any one cell; double fields were searched for exhaustively in view of observations by Cunningham and Speas ('75) in the rat.

To determine if any order was present, the ipsilateral colliculus was divided into two sections, rostral and caudal, such that equal numbers of penetrations were located rostral and caudal to the division. Likewise, the receptive fields were divided into nasal and temporal subgroups such that equal numbers of receptive fields, as determined by the location of the receptive field centers, were located nasal or temporal to the division. If the distribution were random, equal numbers of receptive fields from the rostral section of the colliculus should be found in the nasal and temporal visual field sectors; likewise for the caudal half of the colliculus. For four of the five hamsters, we found a trend such that

nasal visual fields tended to be found in rostral colliculus, and temporal visual fields in caudal colliculus. The remaining hamster showed no trend. The data from only one individual reached statistical significance on this test ( $\chi^2$ ;  $p < 0.05$ ). If data from the five animals are pooled, the hypothesis that visual field position and penetration location in the colliculus are independent can be rejected, at a  $p < 0.05$  level. The data were as follows: The rostral group of penetrations yielded 27 nasal and 17 temporal visual fields; the caudal group of penetrations yielded 14 nasal and 25 temporal visual fields. Therefore there is a low level tendency towards a mirror-symmetric type of topography such that nasal fields are represented rostrally, and temporal fields caudally.

The ipsilateral projection shows a different laminar distribution electro-physiologically than that observed in the normal contralateral projection. Visually responsive cells in the normal contralateral projection are found throughout the entire extent of the superficial gray and optic fiber layers, and in the upper levels of the intermediate gray layer. In the abnormal ipsilateral projection, visually responsive cells are confined to the upper two-thirds to one-third of the superficial gray. In the rostralmost area of the projection, visually responsive cells are found throughout the upper two-thirds of the superficial gray; at the caudalmost border of the projection, visually responsive cells could be located only at the collicular surface.

We undertook a direct comparison of the anatomically traced distribution, and the electrophysiologically recorded distribution of postsynaptic cells by combining electrophysiology and autoradiography in one animal. The animal's eye was injected with tritiated proline and leucine at the nasalmost edge of the eye 24 hours prior to recording.

A reconstruction of the superior colliculi with the positions of penetrations marked, and a chart of the left visual field showing the corresponding receptive field centers, appears in figure 2. The normal contralateral colliculus was mapped completely to determine if any areas of the visual field were rendered unresponsive by the injection. A small area of temporalmost visual field, shown by the dotted outline on the reconstruction, was unresponsive. Since this area of visual field was found only rarely represented on the ipsilateral side in other animals whose ipsilateral

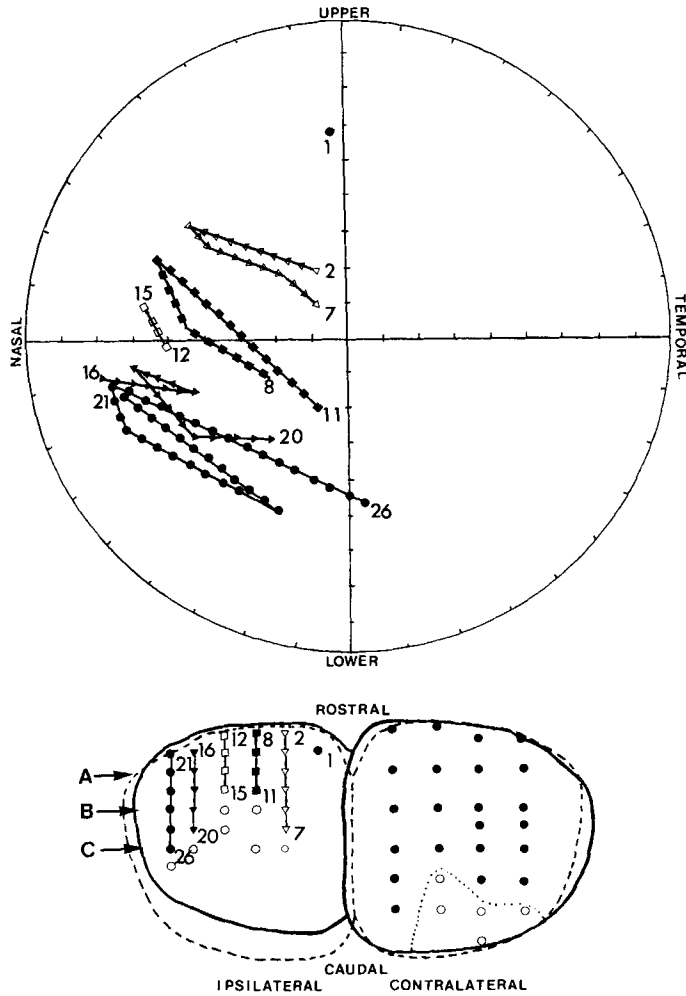


Fig. 2 Positions of electrode penetrations in the superior colliculus, and corresponding ipsilateral receptive field centers for the penetrations made in the left superior colliculus, in a hamster whose right eye was enucleated at birth, and whose remaining eye was injected with tritiated proline-leucine 24 hours prior to recording. The superior colliculi are shown in dorsal view: the broken line corresponds to the normal appearance of the colliculi, and the unbroken line represents the reconstructed appearance of the superior colliculi in this hamster. Open circles indicate penetrations in which no visual response could be obtained; all other symbols indicate penetrations where visual receptive fields could be located. Lines connect rostral to caudal series of penetrations, each series associated with a particular symbol. Corresponding lines of the appropriate symbol connect visual field centers for each rostral to caudal series of penetrations on the visual field map. The visual field is marked off every 10° and is centered on the optic disc. The nasotemporal and upper-lower meridians are defined by the attachments of the extraocular muscles. Arrows A, B, and C indicate the levels at which sections were taken for autoradiography.

projection had been studied, it was assumed that the ipsilateral projection in this animal had been minimally affected, if at all, by the injection. A sample of three dark-field photomicrographs showing both contralateral and ipsilateral colliculus, taken at the levels indicated in the reconstruction of the colliculus,

appears in figure 3. The amount of ipsilateral labelling is clearly much less at all levels than the contralateral labelling. Photomicrograph A is from rostralmost colliculus; units at this level responded vigorously to visual stimulation, and receptive fields were clearly defined. Photomicrograph B is a slightly more caudal

section; units here responded erratically to visual stimulation and receptive fields were ill-defined. In photomicrograph C the only penetrations made were in the lateral part of the ipsilateral colliculus shown, and no visually responsive cells were located in these penetrations. On the medial border, a small re-crossing projection is evident, which happens very infrequently in these cases; no penetrations were made in the area of the small re-crossing projection. Labelling, at all levels observed, is confined to the superficial gray, showing the most extensive distribution rostrally, and the most superficial distribution caudally (with the exception of the small re-crossing projection), which conforms to the distribution seen electrophysiologically.

Grain counts of 100- $\mu$ m sectors centered about electrode penetrations where cells were classed as highly responsive, poorly responsive, or unresponsive were made. Background counts were taken from a subjacent equivalent area in the intermediate gray layer of the colliculus. The ratio of grain counts in highly responsive areas to background was 4.1/1. In poorly responsive areas, the ratio fell to 2.4/1. In the unresponsive areas adjacent to responsive areas, the grain count ratio was 1.7/1, and in caudalmost colliculus where no penetrations were made, the ratio was 1.2/1. The ratio in normal contralateral colliculus (rightmost sector of all 3 micrographs) was not countable due to its extremely high density. Electrophysiological evidence of a sparse projection is thus lost before autoradiographic evidence, but it appears that only a very sparse projection, compared to the normal contralateral projection, is necessary to elicit some type of postsynaptic response.

*Neonatal removal of one eye plus the superficial layers of the ipsilateral superior colliculus*

Similar studies of topography and unit response properties were undertaken in animals in which not only one eye, but also the tectum ipsilateral to it had been removed at birth. After this type of manipulation, fibers of the optic nerve from the remaining eye cross at the optic chiasm and course to the damaged colliculus, with some termination near the surface of the surviving deep tectal layers, and then recross the midline through an abnormal intertectal decussation to innervate the ipsilateral superior colliculus, as shown schematically in figure 4. In addition, since an

eye has been enucleated, there may be also an anomalous ipsilateral projection of fibers following the ipsilateral optic tract.

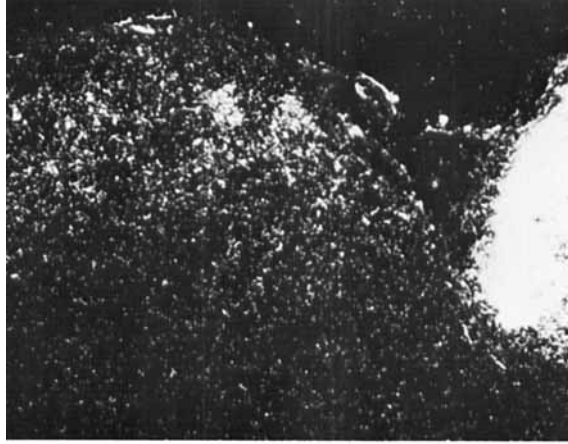
Twelve animals with this type of altered visual system were studied. Of these, eight were completely mapped, and the four others provided partial maps. In every case, a clear topography mirror-symmetric to the normal contralateral projection was observed: upper visual fields were represented medially, lower visual fields laterally, nasal visual fields were represented rostrally, and temporal fields caudally. A reconstruction of a series of penetrations in the ipsilateral superior colliculus and associated receptive fields for one such animal appears in figure 5. On a gross level, there is some malformation of the brainstem; both the inferior colliculus and the remaining superior colliculus intrude into the space opened by the neonatal collicular destruction. This case represents one of the most regular topographies observed in such an animal; only one collicular penetration is associated with an anomalously located receptive field, penetration No. 7.

An estimate of the visual field meridians and contours drawn onto the surface of the reconstructed colliculus appears in figure 6. For this animal, and one other animal in which the topography was sufficiently orderly for computation, deviations of the relative magnification of visual field areas onto the surface of the superior colliculus were computed. Both showed a similar organization. Upper visual field, represented in medial colliculus (from the representation of the optic disc to the upper visual field periphery) was represented on a normal amount of collicular surface (92% for the animal shown; 100% for the other). Lower central visual field, from 0° to 60° relative to the optic disc, was represented on a smaller than normal collicular surface (67% and 54% of normal, respectively). It is interesting to note that this same lower central

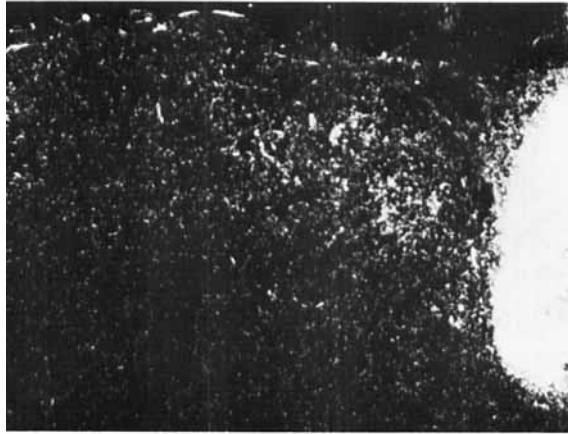
Fig. 3 Dark-field photomicrographs of the pattern of autoradiographic labeling in coronal sections of the superior colliculus from the remaining eye of a hamster monocularly enucleated at birth. Shown is the medial third of the colliculus ipsilateral to the remaining eye (left), the midline, and part of the contralateral colliculus (right). Photomicrographs A, B, and C correspond to sections taken at A, B, and C in figure 2. At level A in the ipsilateral colliculus, receptive fields were well defined and responded briskly; at level B receptive fields were erratic and ill-defined, and at level C, the lateral area shown was unresponsive to visual stimulation. A small re-crossing projection is evident on the medial border; no penetrations were made in this area.



**A**



**B**



**C**

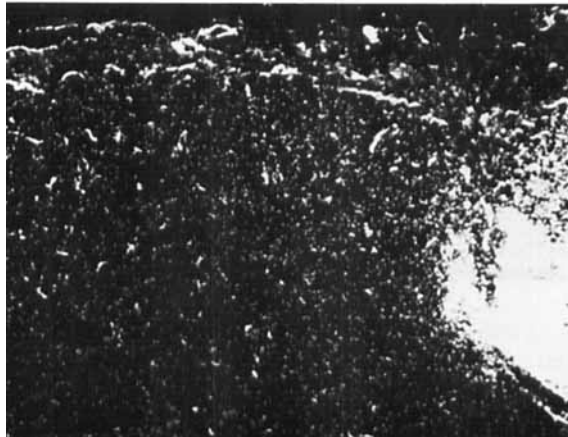


Figure 3

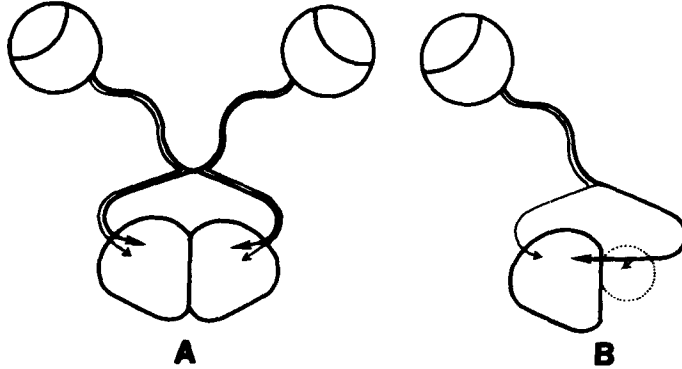


Fig. 4 A schematic dorsal view of the connections of the retinae and colliculi in the normal hamster (A) and in a hamster subjected to monocular enucleation and ipsilateral tectal ablation at birth (B). Shown are the eye (top), optic nerve and optic chiasm, contralateral and ipsilateral optic tract, and the superior colliculi.

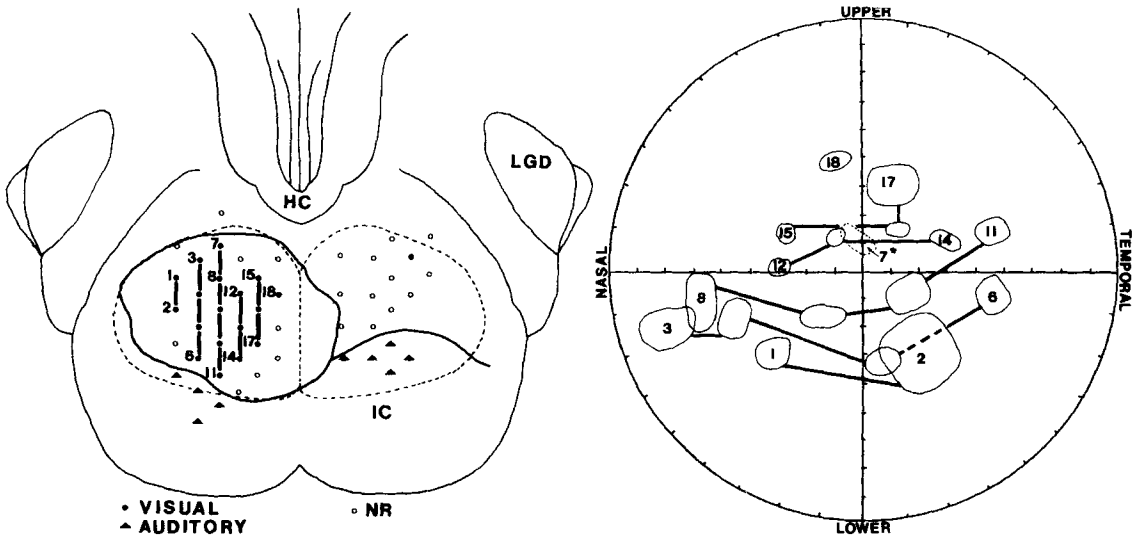


Fig. 5 On the left, a dorsal view of the hamster midbrain, showing both colliculi, surrounding structures and positions of electrode penetrations, and on the right, ipsilateral visual receptive fields corresponding to the numbered penetrations. For the dorsal view of the hamster midbrain, the broken lines correspond to the normal appearance of the hamster colliculi; the heavy lines indicate the appearance from histological reconstruction of the colliculi in this hamster after neonatal unilateral tectum ablation and ipsilateral eye removal. Filled circles correspond to tectal areas where visual responses could be elicited; triangles indicate penetrations where auditory responses were found, and open circles indicate penetrations where no response could be elicited. Bars connect rostral to caudal series of penetrations in visually responsive areas. Corresponding bars connect receptive fields for each rostral to caudal series of penetrations. Field 7, marked with a star, is topographically misplaced. The visual field is marked off every 10° and is centered about the optic disc. The nasotemporal and upper-lower meridians are defined by the attachments of the extraocular muscles. Abbreviations: HC, habenular commissure; LGD, dorsal lateral geniculate body; IC, inferior colliculus.

visual field, in both of these animals, showed evidence of representation also on the other side of the midbrain, in the remaining deep layers of the neonatally damaged colliculus. The lower periphery of the visual field, by contrast, showed expansion of its surface representation three to six times normal.

The positions of the meridians, as defined by the naso-temporal and upper-lower rectus

muscle insertions, in all animals were undistinguishable from normal.

Although the general topography of this projection was constant from animal to animal, gaps in the representation of the visual field, misplacements of parts of the visual field representation, and local inversion along both the rostrocaudal and mediolateral axes were common and varied in amount from ani-

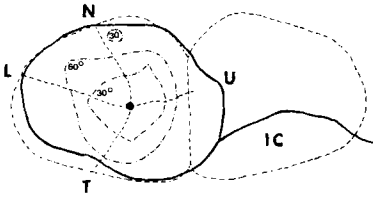


Fig. 6 A projection of the horizontal and vertical meridians and isocontour lines relative to the optic disc onto the surface of the ipsilateral superior colliculus for the hamster with the recrossing projection shown in figure 5. The normal appearance of the colliculi are shown with the dashed lines; the reconstructed appearance of the colliculus is shown with solid lines. The optic disc, at the center of the map, is represented by a large dot. Contour lines, containing the fields found 30° and 60° from the optic disc, are shown as broken lines (- · - · -). The nasotemporal meridian, NTM, and the upper-lower meridian, ULM, are represented with the light dashed lines (- - -).

mal to animal. Six of the eight studied showed at least one inversion between neighboring penetrations on the mediolateral axis in their associated receptive fields on the upper-lower visual field axis. Seven of the eight animals showed at least one inversion on the rostro-caudal, nasotemporal axis. In four penetrations, in two different animals, misplaced fields of the following type were observed: as the electrode first contacted the superficial gray layer, a severely dislocated field was observed, but as the electrode was lowered into the deeper part of the superficial gray, the field moved back to a more appropriate topographic position. This phenomenon probably corresponds with a pattern seen in Fink-Heimer degeneration material in similar cases with small retinal lesions made in adulthood: small, isolated superficial patches of terminal degeneration were observed at locations considerably removed from other areas of terminal degeneration (Schneider and Jhaveri, '74; see also fig. 7).

In six animals, the remaining projection to the deep layers of the neonatally damaged colliculus was studied and compared to the visual field representation in the recrossing projection. In four of the six cases, the spared contralateral projection corresponded to a full or partial scotoma in the recrossing projection; in the remaining two cases the contralateral projection and the recrossing projection showed complete overlap. These scotomas in the recrossing representation were in three cases associated with spatially separated visual receptive fields bracketing the scotoma for single neurons in the ipsilateral colliculus.

The pattern and amount of disorder observed using electrophysiological techniques is similar to that described using neuroanatomical degeneration techniques (Schneider and Jhaveri, '74). Figure 7 shows a dorsal view reconstruction of the terminal degeneration caused by a lesion restricted to part of the lower retina. This lesion was made 48 hours prior to recording, so that the order in the remaining representation of the visual field and the distribution of the lower nasal retina projection could be compared. Also shown in figure 7 is a similar view of the colliculi in a normal brain, showing the area of terminal degeneration that would be expected to result in a case with such a retinal lesion, as judged by a reconstruction of the observed pattern of degeneration in the dorsal nucleus of the lateral geniculate body (Frost and Schneider, '79; Jhaveri and Schneider, '74). There is considerable terminal degeneration in the area corresponding to the expected mirror image location, but there are also a number of patches of terminal degeneration located outside this region.

A reconstruction of the same left superior colliculus showing a series of penetrations, and a chart of the left visual field with the correlated receptive field centers, appear in figure 8. This map shows considerable disorder, and the expected upper-temporal scotoma due to the retinal lesion (compare fig. 12), yet the general mirror-symmetric pattern is evident: lower visual field is represented in lateral colliculus; upper visual field in medial colliculus; nasal field in rostral colliculus, and temporal field in caudal colliculus. There is an area in central visual field that shows both an upper-to-lower and nasal-to-temporal inversion in its representation on the colliculus. Displaced projections, similar to the major displaced focus from *intact* portions of the retina, could account for the type of disorder seen in the recorded map. Some of the scattered projections may be too small for reliable driving of tectal units.

#### *Receptive field properties*

Receptive field properties observed in this and other cases, for units near the midline close to the point of entry of the abnormal decussation, were nearly normal. Units responded briskly to moving or flashed stimuli, and would respond to both dark stimuli on light backgrounds or light stimuli on dark backgrounds. Spontaneous activity was low. Occasionally, directionally sensitive units

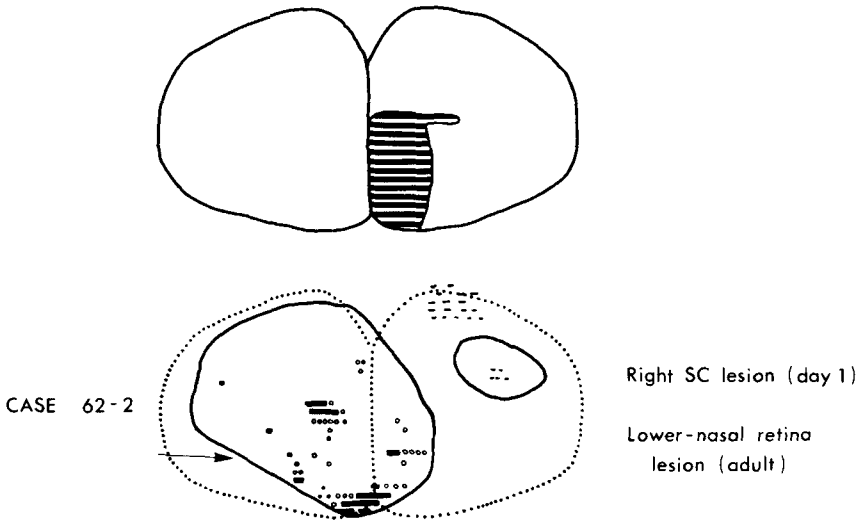


Fig. 7 A comparison of the degeneration observed after a lower nasal retinal lesion in the normal hamster, in the contralateral colliculus, and the degeneration after the same lesion observed in the ipsilateral colliculus in a hamster subjected to ablation of the right superior colliculus, and enucleation of the right eye at birth (below). The upper figure shows the pattern of degeneration expected in a normal hamster with this size of retinal lesion; the lower figure shows the actual pattern of degeneration observed. The dotted line shows the normal appearance of the superior colliculus; the solid lines show the actual appearance of the colliculus in this hamster. Open circles refer to terminal degeneration deep to the colliculus surface; filled bars to terminal degeneration throughout the superficial gray.

were encountered. Units responded without habituation to repetitive stimulation. Near the midline, the sizes for receptive fields were somewhat larger than normal, with a mean diameter of  $16^\circ$ , ranging from  $10^\circ$  to  $30^\circ$ . The mean size of receptive fields for this area is normally  $8^\circ$ , ranging from  $3^\circ$  to  $15^\circ$ . According to neuroanatomical findings, the retinal projection to this region is of normal density (Schneider, '73).

In caudal and lateral colliculus, receptive fields were still larger, averaging  $21^\circ$  (range  $13^\circ$ - $37^\circ$ ). These units tended to habituate or respond erratically to repeated stimulation; also, the receptive field borders were ill-defined. In the lateralmost colliculus, areas unresponsive to visual stimulation were often found, as illustrated in figure 12. The anatomical studies show that the retinal input to the lateralmost part of the left superior colliculus in these cases is very sparse (Schneider, '73; So and Schneider, '78).

Visual receptive fields could often be mapped for units in the area of the damaged right colliculus; the extent of this recordable input varied markedly from animal to animal. Visual receptive fields were highly abnormal: fields were often very large (figs. 10, 12),

sometimes encompassing whole quadrants or hemifields. Spontaneous activity was often high in contrast to the superficial gray layer. Frequently, units were found that responded in a manner resembling units in the pretectal nuclei of the normal hamster; they had large receptive fields in which both moving or stationary stimuli would elicit a vigorous sustained response, but they would also respond in a tonic excitatory fashion to increases in ambient illumination. Very little consistent topography was ever observed in the damaged collicular area: no naso-temporal topography was ever apparent, but in two cases the data indicated some upper-to-lower field order on the mediolateral axis of the brain, as in figure 12B.

#### *Neonatal posterior cortex ablation and retinotopic organization of the recrossing retinotectal projection*

In two animals, on the day of birth posterior cortex ablation was added to removal of the right eye and ablation of the superficial layers of the right superior colliculus. Since it is known that the visual cortex projects in a topographic manner to the superior colliculus (Lund, '66; McIlwain, '73), we were interested

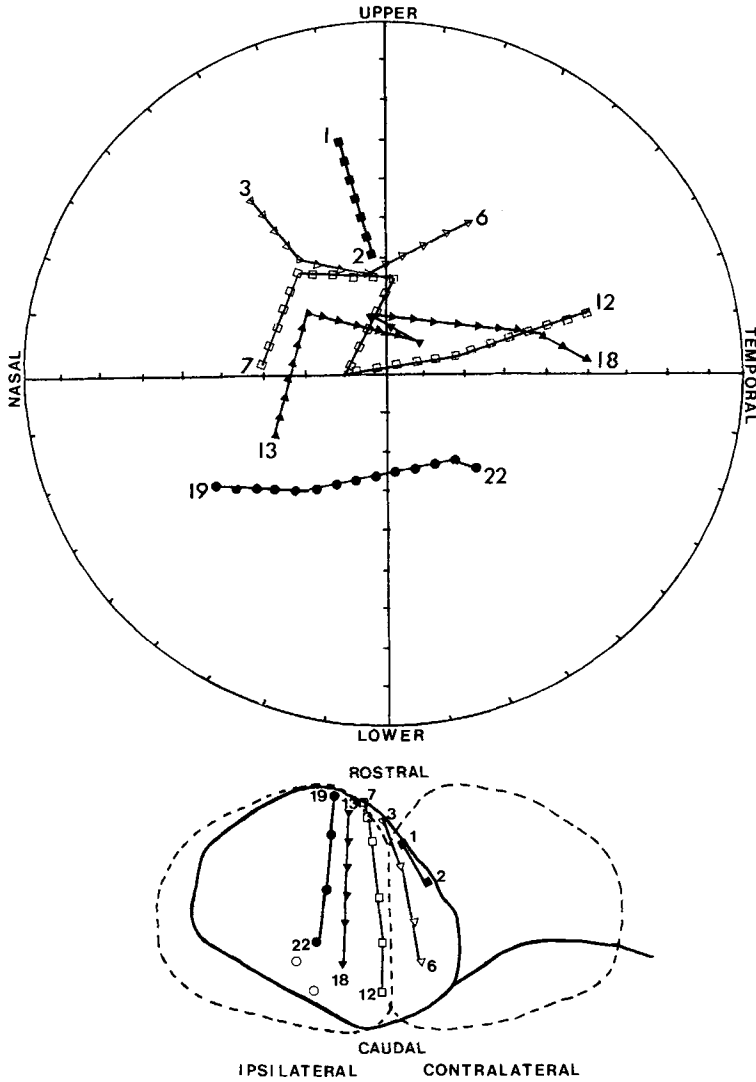


Fig. 8 Positions of electrode penetrations into the superior colliculus, for the hamster described in figure 7. At maturity, prior to recording, a lesion had been made in lower nasal retina. The superior colliculi are shown in dorsal view: the broken line corresponds to the normal appearance of the colliculi, and the unbroken line to the reconstructed appearance of the superior colliculi in this hamster. Lines connect rostral to caudal series of penetrations, each series associated with a particular symbol. Corresponding lines of the appropriate symbol connect visual field centers for each rostral and caudal series of penetrations on the visual field. The visual field divisions = 10°, and the visual field is centered about the optic disc. The nasotemporal and upper-lower meridians are defined by the attachments of the extraocular muscles.

in any possible effect that removal of this projection might have on the development of ordered retinotectal topography. The removal of visual cortex had no effect on the visual field representation observed in the ipsilateral colliculus: an organization mirror-symmetric to the topography of the normal contralateral projection was observed, with a degree of dis-

order in both cases which was well within the variability observed in cases with no neonatal cortical lesion.

*The relationship of visual orienting behavior and retinotectal topography in animals with anomalous recrossing projections*

Visual orienting behavior, assessed by a

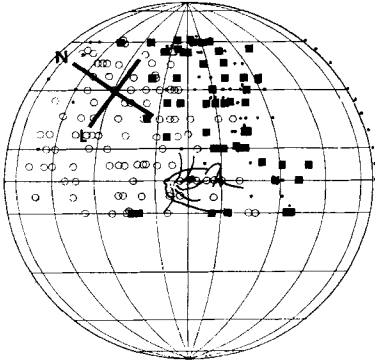


Fig. 9 A profile of the visually elicited orienting movements in a hamster with neonatal unilateral tectal ablation and monocular enucleation to stimuli presented to the designated locations in its visual field. The map is centered about the hamster's eye and the long axis of the hamster's body; the map is marked off in  $20^\circ$  intervals. For reference to the electrophysiology maps, the crossed bars indicate the approximate position of the optic disc and the meridians created by the eye muscle attachments; thus, the nasal field of the eye is upper-nasal with respect to the head. Open circles indicate visual field locations where the hamster turned in the correct direction to get a sunflower seed. Black dots indicate stimulus positions where no response was elicited. Filled squares represent wrong direction turns.

videotape analysis of turning movements in response to sunflower seeds presented in various locations in the visual field of the stationary animal, was studied in 24 hamsters. Fifteen of these animals had undergone removal of one eye and ablation of superficial layers of the ipsilateral superior colliculus at birth. Detailed electrophysiology was done in two of them. Similar studies were carried out with two hamsters which had only a unilateral eye removal at birth, four with one eye removed in adulthood, and three controls.

Hamsters with removal of one eye alone showed normal visually elicited turning movements under our test conditions. However, the animals with an additional lesion of the ipsilateral superior colliculus showed a more complex but consistent pattern of orienting (figs. 9, 11).

Correct direction turns were made to sunflower seeds presented in the lower and lower nasal visual field (in this case "lower" and "lower nasal" refer to true horizontal and vertical relative to the hamster's head and to gravity, unlike the coordinates used for electrophysiology, which were based on retinal positions, oriented with respect to eye-muscle insertions). In upper and upper temporal vis-

ual field, the animal frequently turned contralaterally, i.e., in the wrong direction, when presented with a seed. Though this pattern of elicited correct and incorrect direction turns was the same in all animals, the amount of upper-temporal visual field in which incorrect direction turns could be elicited varied markedly from animal to animal, as shown by a comparison of figures 9 and 11.

The map of visual turning behavior shown in figure 9 conforms in a general way to the pattern of visual field representation recorded in the ipsilateral colliculus (fig. 10A) and in the residual deep layers of the damaged contralateral colliculus (fig. 10B) in the same animal. The crossed bars in the behavioral map indicate the approximate position of the projection of the optic disc and the meridians created by the lines connecting the rectus muscles, so that the electrophysiological maps and the maps of visual orienting can be compared. Note that the nasal field using physiology coordinates in upper-nasal on the map of visual orienting behavior. This animal showed wrongway turning throughout his upper visual field (in physiology coordinates), and correct direct turns in most of his lower visual field. The behavioral map delineates general visual field areas only, since the hamster's eye movements are not recorded in this procedure. Three similar maps for other hamsters have been published previously (Schneider, '73; Schneider and Jhaveri, '74).

In the electrophysiological maps, the visual field is represented nearly completely, in a fairly orderly fashion, in the ipsilateral colliculus, with the exception of a partial scotoma in the lower field (this animal had dual receptive fields for single units which bracketed the scotoma). The upper visual field, particularly the upper temporal visual field, is heavily represented, with nearly normal receptive field sizes and unit response properties. This ipsilateral representation of the upper visual field can account for the wrong way turning observed in the upper visual field of this animal.

Represented in the remaining deep layers on the contralateral side is a patch of upper temporal visual field, but the predominant visual field area represented is the lower central area. Although the receptive fields are large and topographically disorganized, this projection could account for the correct-direction turns to stimuli presented in the animal's lower visual field.

The profile of visual orienting behavior and the visual field representation in the colliculi for a second animal appears in figures 11 and 12. This animal showed a much more restricted area of wrong-direction turning, confined to less than 20° of upper temporal field, and showed correct direction turns in response to stimuli in the remainder of its visual field. However, the entire ipsilateral colliculus was innervated in a very orderly fashion; the strongest, most normal receptive fields again appeared for units in the medial tectum. Units sensitive to visual stimulation in the residual colliculus which had been damaged at birth were sparse, topographically disorganized, and responded erratically to visual stimulation. Thus, on the basis of these electrophysiology data, one would predict more wrong-direction turning and less correct-direction turning than we actually observed in this particular hamster. Variables not examined in these experiments must be important; these may include effects of activity in other structures of the visual system, interactions between the two colliculi, and effects of learning.

DISCUSSION

*The consequences of neonatal removal of one eye*

The hamster, like the rat and the rabbit, shows an increased ipsilateral projection from the remaining eye to the superior colliculus after neonatal monocular enucleation. As in the rat (Cunningham and Speas, '75), this projection appears to be functional in that good

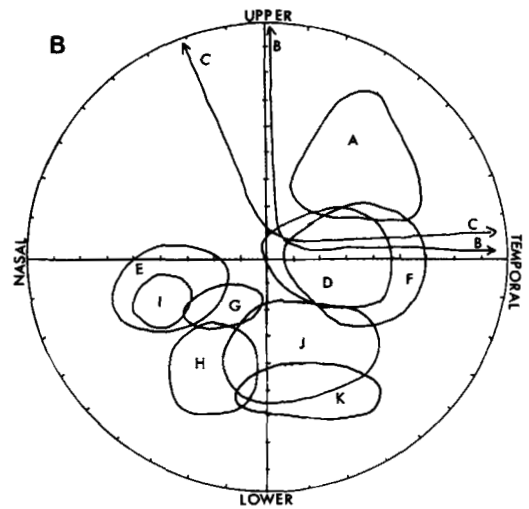
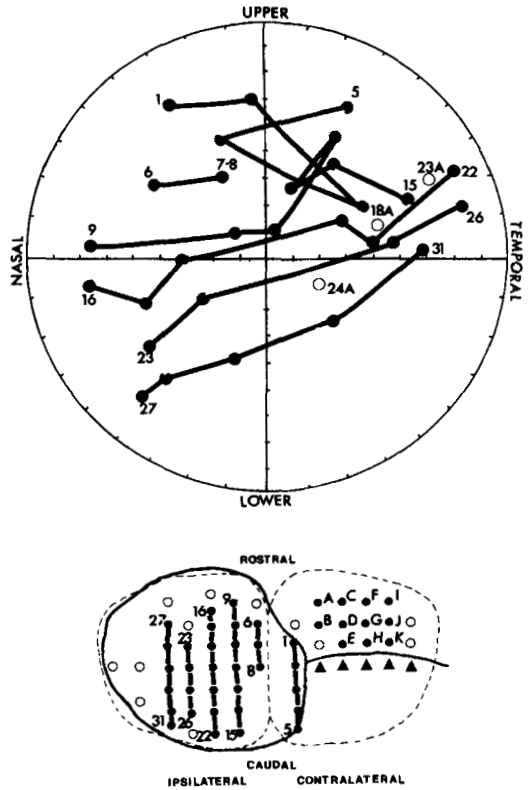


Figure 10

Fig. 10 Ipsilateral visual field centers (A), contralateral visual fields (B) and associated penetrations in the superior colliculus of the hamster whose visual orienting behavior was described in figure 9. For the colliculus diagram, dashed lines indicate the normal appearance of the colliculus, and the solid lines indicate the actual appearance of the collicular area in this hamster. In the ipsilateral colliculus, open circles indicate penetrations where no visual response could be elicited; filled triangles indicate areas of auditory response. Filled circles correspond to penetrations where visual receptive fields were located; lines connect rostral to caudal series of penetrations. Corresponding lines link receptive field centers (A), indicated by large black dots, for rostral to caudal penetration series. Penetrations 18, 23, and 24 were associated with dual receptive fields, and are represented both by the appropriate black dot in the rostral to caudal series, and an additional marked open circle. Receptive fields marked by letters for the contralateral projection appear in B. The visual field is marked off every 10° and is centered about the optic disc. The nasotemporal and upper-lower meridians are defined by the attachments of the extraocular muscles.

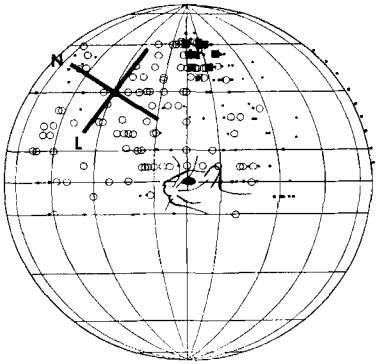


Fig. 11 A profile of visually elicited orienting movements in a second hamster with neonatal unilateral tectal ablation and eye enucleation. The map is centered about the hamster's eye and the long axis of the hamster's body; the map is demarcated in 20° intervals. For reference to the electrophysiology maps, the crossed bars indicate the approximate position of the optic disc and the meridians created by the eye muscle attachments. Open circles (○) indicate correct direction turns to a stimulus. Black dots (•) indicate stimulus positions where no response was elicited. Filled squares represent wrong direction turns. Ambivalent right-way then wrong-way turns are represented by filled circles within squares.

postsynaptic visually elicited responses can be obtained from cells in the rostral half of the ipsilateral colliculus. Since both the rat and the hamster are more immature than the rabbit at birth (Chow et al., '73; Lund and Miller, '75), the hypothesis that the maturity of the rabbit at the time of unilateral eye removal is responsible for the inability of its abnormally increased ipsilateral projection to reliably drive postsynaptic elements seems plausible. It may be that these projections are simply too sparse in the rabbit for reliable functional effects, though the possibility of non-functional synapses is difficult to eliminate.

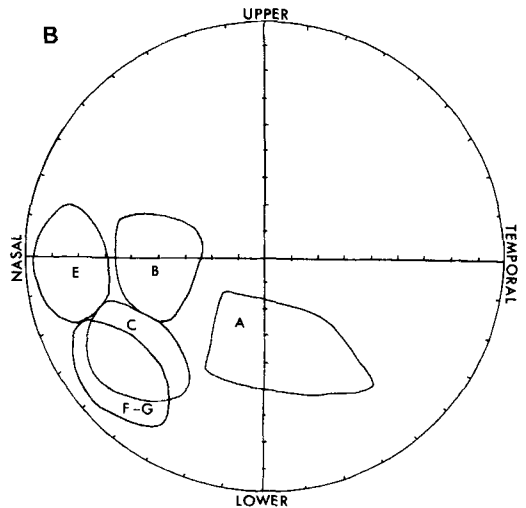
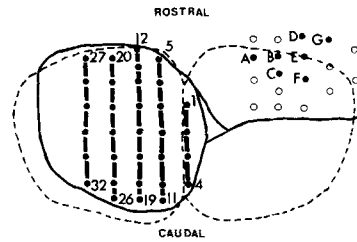
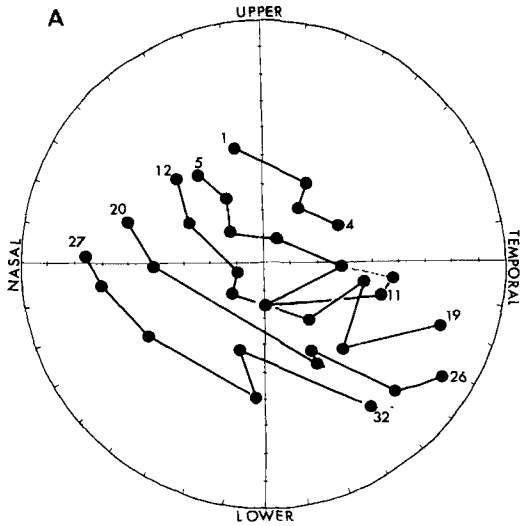


Figure 12

Fig. 12 Ipsilateral visual field centers (A) contralateral visual fields (B) and associated penetrations in the superior colliculus of the hamster whose visual orienting behavior was described in figure 11. For the colliculus diagram, dashed lines indicate the normal appearance of the superior colliculus, and the solid lines indicate the actual appearance of the collicular area in this hamster. In the ipsilateral colliculus, open circles indicate penetrations where no visual response could be elicited. Filled circles correspond to penetrations where visual receptive fields were located; lines connect rostral to caudal series of penetrations. Corresponding lines link receptive field centers (A), indicated by large black dots, for rostral to caudal penetration series. Receptive fields marked for the contralateral projection appear in B. The visual fields are marked off every 10° and are centered about the optic disc. The nasotemporal and upper-lower meridians are defined by the attachments of the extraocular muscles.



Multiple factors may contribute to the expression of retinotectal topography in this sort of anomalous ipsilateral projection, the ipsilateral projection may consist of two distinct fiber populations, the normal, sparse ipsilateral projection, hypertrophied to innervate a larger area of the ipsilateral colliculus (Goodman et al., '73), and a second group of fibers, that under normal conditions would have gone contralaterally but were diverted, or underwent collateral sprouting at the optic chiasm as a result of the eye removal (Cunningham and Speas, '75; Lund et al., '73; Lund and Miller, '75). There is anatomical support for the second hypothesis (Cunningham, '76; Frost and Schneider, '76).

The consequences of such a dual innervation stem from the likelihood that the normal ipsilateral optic tract follows different rules of topography than the normal contralateral projection, in order to keep the projections from the two eyes in functional register. As one moves from rostral to caudal in the colliculus, the corresponding positions in the contralateral eye move from temporal to nasal. In order for the visual receptive fields to be in register, the matching positions in the ipsilateral eye must proceed from nasal to temporal, in the temporal margins of the ipsilateral retina. Thus, if there is a topography in the rostrocaudal extent of the normal ipsilateral projection, it must follow different rules of termination, with respect to the nasotemporal retinal axis, than the normal contralateral projection.

Alternatively, one might imagine that the normal ipsilateral projection is sufficiently restricted in its nasal to temporal angular extent ( $40^\circ$  to  $60^\circ$ ) that the rostrocaudal axis need not be specified. The upper to lower topography, on the other hand, would be expected to follow the contralateral system of projection in any case.

The general disorder of the rostrocaudal axis in these animals, and the observation of local areas of ordered termination, some displaying one polarity and others the opposite, can be explained by the hypothesis that two fiber populations, with different patterns of termination, interact to create the disordered topography observed. The significant, slight trend for the expression of the contralateral type of termination may reflect the relative proportion of the two fiber types in the population.

#### *Properties of units driven by abnormally sparse projections*

A relatively sparse amount of termination, as seen using autoradiographic techniques, appears to be sufficient to allow reliable postsynaptic visually elicited responses. The sparse terminations in both types of abnormal ipsilateral projections appear to be correlated with a distinct set of single-unit response properties in the colliculus. Receptive fields are ill-defined in that the progression from the area eliciting near-maximum response and the area eliciting no response is graded over  $5^\circ$ - $15^\circ$  rather than the normal  $1^\circ$ - $5^\circ$ . Excitatory terminals of each axon may be spread over a wider tectal area than normal, arborizing in the superficial part of the superficial gray rather than arborizing in narrow columns perpendicular to the collicular surface; this morphology would decrease the excitatory convergence on single tectal cells. In addition, a suppressive surround has been hypothesized for visual receptive fields in the colliculus of several species, in that the optimal stimulus for most colliculus cells is the same size or smaller than the activating region (Cynader and Berman, '72; Dräger and Hubel, '75, '76; Sterling and Wickelgren, '69). The larger receptive field sizes observed in the areas of sparse termination and the ill-definition of borders may also be due to the lack, or a lesser definition of, the normal suppressive surround.

Another distinguishing property of cells in areas of sparse terminations is the tendency for responses to show habituation after repeated stimulation, and to be erratic in general. Lack of response habituation and the general robustness of unit response may be related in a direct way to the degree of excitatory convergence.

#### *The nature of the polarity cue*

A major issue in studies of the development or regeneration of topographically ordered retinotectal connections is the nature of the cues which guide the growing axons. Various possibilities have been considered in studies of fish, amphibians and birds (see reviews by Gaze, '74; Meyer and Sperry, '76; Keating, '76). It is interesting to consider the sources of information which may be important in addition to any specific fiber-to-tectal-cell matching (chemospecificities) that may occur. Such in-

formation could be provided by the direction of entry of retinal fibers into the tectum, the relative timing of maturation of retinal and tectal cells, or the retinotopic order in the optic tract as it enters the tectum.

During normal development, incoming retinal fibers enter the colliculus from the rostral and rostrolateral margin. Cellular maturation in rostral tectum slightly precedes maturation in caudal tectum during the time innervation is proceeding (Frost, '75). In the adult hamster, the optic tract enters the rostral end of the colliculus as a broad sheet of fibers, within which the upper-lower retinal axis has a topographic representation (fibers from upper retina are lateral and those from lower retina are medial in the brachium of the superior colliculus) (Jhaveri and Schneider, '74); it is thus probable that these fibers enter in an orderly fashion during development.

In the case of an anomalous ipsilateral projection created by an abnormal intertectal decussation, all of these normal developmental patterns are disturbed. Innervation proceeds from the medial wall of the colliculus, 90° from the normal path. Innervation of the ipsilateral colliculus is retarded relative to the time course of normal maturation (So, '78), and thus close timing of the maturation of retina and colliculus is reduced as a factor contributing to the topography. Orderly representation of the upper-to-lower retinal axis in the optic tract as it reaches the tectum is disturbed within the abnormal recrossing fiber bundle (Schneider, unpublished data). These findings confirm in a mammal the finding in experiments with goldfish that preservation of normal retinotopic order is not dependent on the path taken by the entering fibers (Arora and Sperry, '62). The presence of a topography mirror-symmetric to the normal contralateral topography indicates there must be a polarity cue in the tectal tissue acting independently of the maturational factors mentioned. The source of this cue is not known. The presence of this polarity cue does not obviate the importance of the other factors in affecting the details of the map, as indicated by the disorder within the abnormal projections.

#### *Sources of disorder in anomalous projections*

The evidence of some retinotopic disorder in the anomalous ipsilateral projections shows that locus-specific or polarity cues are not absolute. It appears that the mechanical disrupt-

tion of axonal trajectories results in some disorder in the final map, as indicated also by the neuroanatomical studies reported by Jhaveri ('73), Schneider and Jhaveri ('74), and Miller and Lund ('75). In addition, in regenerative nervous systems, reorganization of topographic projections requires time for completion (Udin, '77; Jacobson and Gaze, '65). In the hamster, however, the rearrangement of axon endings within the tectum apparently ceases at a critical age (So and Schneider, '78) thus the map could become "frozen" before it becomes fully orderly.

The anomalous recrossing projection does make normal, functional synapses, as evidenced by the normal receptive field properties of cells in the ipsilateral colliculus. This is also supported by the finding of visually elicited turning in the wrong direction, which can be abolished by cutting the recrossing bundle of fibers in the adult hamster (Schneider, '77). It is not certain, however, whether every fiber group observed using anatomical tracing techniques has made excitatory connections sufficient to drive postsynaptic units. We have the impression that the topography observed from tracing the degeneration patterns in the ipsilateral colliculus after small retinal lesions is less regular than that seen electrophysiologically. However, every major type of error in topography observed using anatomical techniques, such as gaps in the retinal representation, patches of isolated superficial degeneration, misplaced terminal areas, and representations of separated retinal areas in single collicular areas, has been observed electrophysiologically as well.

In the case of anomalous ipsilateral innervation created by recrossing fibers after unilateral eye removal and ablation of the homolateral tectum, an enhanced ipsilateral projection through the ipsilateral optic tract due to the eye removal may exist as well, and may be a source of disorder in the observed retinotopic maps. However, the enhanced ipsilateral pathway traveling through the ipsilateral optic tract, representing primarily temporal retina, does not appear to be a major source of disorder; no more disorder in the retinotectal topography appears in nasal visual field than in temporal visual field. However, this ipsilateral projection arising at the chiasm is much sparser than the recrossing projection, and may arrive later in development (Frost, '75; Schneider, '73; So and Schneider, '76, '78).

In the anomalous projection to the residual deeper layers of the superior colliculus after a

neonatal lesion, our electrophysiological data show a functional but very disorderly projection. Although there is a substantial retinal projection, no clear topography was ever observed in the nasotemporal axis of the visual field, and there was only a hint of upper to lower topography in some of the animals. Thus, the presence of the superficial gray layer may be critical for the expression of at least the nasotemporal axis of the retinotopic projection. However, it should also be noted that the total area of tectal termination is markedly reduced in these cases. The total size of the termination area is another factor that may influence the development of topography in the optic tract projection.

*Anomalous ipsilateral projections and visual orienting behavior*

Visually elicited turning behavior shows a good general correlation with the electrophysiologically observed retinotectal topography. Visually elicited turning in the wrong direction is strongest in the upper visual field of the remaining eye, where the recrossing projection is the most dense and single unit response properties are the most normal. No misdirected visual orienting occurs that does not have a plausible correlate in the ipsilateral visual projection.

Correlated with the correct-direction turns these hamsters can make, we have found only a very disorganized contralateral retinal projection to the residual colliculus. In some cases, the same visual field areas are represented both contralaterally and ipsilaterally, which indicates that these two projections must compete for control of orienting behavior. In many animals there was a sizeable part of the visual field where stimuli could elicit turns in either direction. In addition, some turns elicited from this area of overlap were begun in one direction, but then the animal stopped and reversed himself (fig. 11; and Schneider, '73).

The correct-direction turns often did show evidence of control by an abnormal neuronal system, for some of them were distinctly inaccurate, slow or clumsy (Schneider, '77, and unpublished). Undershooting and overshooting of the stimulus occurred, for example. Nevertheless, the possible roles of pathways other than the retinotectal in the control of turning movements must be considered. Such pathways include those arising in visual cortical areas and projecting to superficial tectal layers (Ingle and Sprague, '75), and a pathway

from the ventral nucleus of the lateral geniculate to the superior colliculus, including the deeper layers (Graybiel, '74). Another candidate is the route from the substantia nigra to the superior colliculus (Graybiel and Sciascia, '75; Rinvik et al., '76), which comes from a nigral area receiving input from a part of the corpus striatum which in turn receives input from visual cortex (Faull and Mehler, '76). Although visual system pathways other than those to the superior colliculus do not appear to be sufficient for the visually guided behavior we are considering (Schneider, '69, '70, '77; So, Schneider and Ayres, in preparation), they may augment, or interact with, visual orienting mediated by the superior colliculus.

The extent to which rodents may recalibrate their visual orienting behavior when systematic errors between visual field location and evoked head movements occur is unknown. Certainly, some degree of suppression of incorrect orienting movements which are never rewarded by target acquisition is likely. All of these sources of plasticity in visuomotor organization, anatomical, physiological and behavioral, suggest interesting new avenues for further research.

ACKNOWLEDGMENTS

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