Anomalous patterns of callosal connections develop in visual cortex of monocularly enucleated hamsters

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In this study we analyzed the effect of neonatal monocular enucleation on the pattern of callosal connections in striate cortex of the golden hamster. Callosal connections were revealed in the hemisphere ipsilateral to the remaining eye following multiple injections of either the enzyme horseradish peroxidase or the fluorescent tracer Fluoro-Gold into the contralateral hemisphere.
The most salient anomaly induced by the removal of one eye at birth is the appearance of a dense band of callosal connections that runs anteroposteriorly in medial portions of striate cortex. No obvious changes in the laminar distribution of callosal connections were observed. Comparison of our present results with those obtained by Olavarria ***et al*** *(1987) in monocularly enucleated rats reveals that neonatal enucleation induces remarkably similar anomalies in the callosal patterns of rats and hamsters. This similarity suggests that the role the eyes play in the development of the visual callosal pathway is similar among rodent species. Moreover, the finding of an anomalous callosal band in striate cortex one-eyed hamsters supports the notion that disruption of visual input does not arrest callosal development, but rather leads to the development of entirely new features in the callosal pattern.*

Key terms: *corpus callosum, development, rodent, visual cortex.*

INTRODUCTION

The highly organized patterns of cortico-cortical connections observed in the neocortex of adult mammals represent the final stage of developmental processes that reshape the widespread, immature connections present in neonates. A pathway in which these changes have been extensively studied is the interhemispheric connection through the corpus callosum (reviewed by Innocenti, 1991). For instance, in neonatal rats, callosal cells are distributed uniformly throughout occipital cortex, but by the end of the second postnatal week the adult visual callosal pattern can be clearly recognized (Olavarria and Van Sluyters, 1985).

Investigations of the mechanisms guiding the development of callosal connections have revealed that this pathway can be significantly altered by disrupting the pattern of retinal projections in the neonate (see Innocenti, 1991). Previous studies in rodents (hamster: Rhoades and DellaCroce, 1980b; Fish *et al*, 1991; rat: Rothblat and Hayes 1982; Lund *et al*, 1984), lagomorphs (Murphy and Grigonis, 1988), and carnivores (Innocenti and Frost, 1980) have reported that removal of one or both eyes at birth produces a mature pattern in which callosal cells and terminations in occipital cortex are more widely distributed than in normal individuals.

The resemblance that this wide distribution has to immature stages of callosal

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development (see Innocenti, 1991; Olavarria and Van Sluyters, 1985) led to the suggestion that neonatal disruption of visual input arrests the normal developmental process (*e.g.*, Rhoades and DellaCroce, 1980b; Rothblat and Hayes, 1982; Murphy and Grigonis, 1988). However, it is difficult to reconcile this idea with the observation of Olavarria *et al* (1987) in the rat that neonatal monocular enucleation leads to the appearance of a band-like accumulation of callosal connections in medial striate cortex, a region which normally has few callosal connections in the adult (see also Cusick and Lund, 1982). Since a callosal band in middle portions of striate cortex is never observed during normal callosal development (Olavarría and Van Sluyters, 1985), its appearance in enucleated rats suggests that disruption of visual input does not arrest callosal development, but rather leads to the development of entirely new features in the callosal pattern.

In an attempt to clarify the role played by the eyes on callosal development across species, we decided to investigate the effect of monocular enucleation on the callosal pattern in other rodent species. We chose the hamster (family Cricetidae) because it is more distantly related to the rat (family Muridae) than other commonly used laboratory rodents. There is also evidence that the overall pattern of visual callosal connections in the hamster shows consistent differences with that in the rat, especially in lateral extrastriate cortex (Olavarria and Montero, 1990). Finally, we wanted to capitalize on what is known in the hamster about the organization and development of the visual callosal pathway, as well as on the effects of enucleation on subcortical visual nuclei (Dursteler *et al*, 1979; Thompson, 1979; Finlay *et al*, 1979; Rhoades and DellaCroce, 1980a,b; Rhoades, 1980; So and Jen, 1982; So *et al*, 1984; Fukuda *et al*, 1984; Olavarria and Montero, 1990; Trevelyan and Thompson, 1992).

Our results demonstrate that, contrary to previous reports, the callosal pattern in monocularly enucleated hamsters presents distinct anomalies that are quite similar to those reported in one-eyed rats by Olavarria *et al* (1987). Specifically, monocularly enucleated hamsters developed an extra callosal band in medial portions of striate cortex ipsilateral to the remaining eye. These results suggest that the role that retinal input plays in the development of the callosal pathway is similar among rodent species. Some of these data have been presented previously as an abstract (O'Brien *et al*, 1992).

METHODS

The present study is based on data obtained from 35 golden hamsters (*Mesocricetus auratus*). On the day of birth, 29 hamsters underwent monocular enucleation under Halothane anesthesia (2-5% in O_2). The remaining six hamsters were used as normal adult controls.

We studied the distribution of visual callosal connections revealed by either the anterograde and retrograde transport of horseradish peroxidase (HRP; Sigma Type VI 30% in dH_2O), (n = 28), or the retrograde transport of the fluorescent tracer Fluoro-Gold (Fluorochrome Inc., 2-4% in dH_2O), (n = 7). Animals (1-6 months old) were anesthetized with Halothane (1.5% - 5% in O_2) or Equithesin (0.3ml/ 0.1kg ip), and a total of 1.5 - 2.0 µl of tracer was injected into 15-20 sites spaced evenly across the posterior surface of one hemisphere. After 24-48 hours animals injected with HRP were administered a lethal dose of pentobarbital (50 mg/kg ip) and perfused transcardially with 0.9% saline followed by 2% glutaraldehyde in 0.1 M phosphate buffer. Animals injected with Fluoro-Gold survived 72 hours and were perfused similarly with 4% paraformaldehyde in 0.1 M phosphate buffer. All animal procedures were performed according to N.I.H. guidelines (N.I.H. Publication No. 85-23, Revised 1985) and protocols approved by the animal care committee at the University of Washington, Seattle.

Brains were removed from the cranium and either left intact for coronal sectioning or flattened for tangential sectioning (Olavarria and Van Sluyters 1985). The blocks of tissue were left overnight in 20% phosphate buffered sucrose (0.1 M), and then sectioned at 40-60 µm on a freezing microtome. Sec-

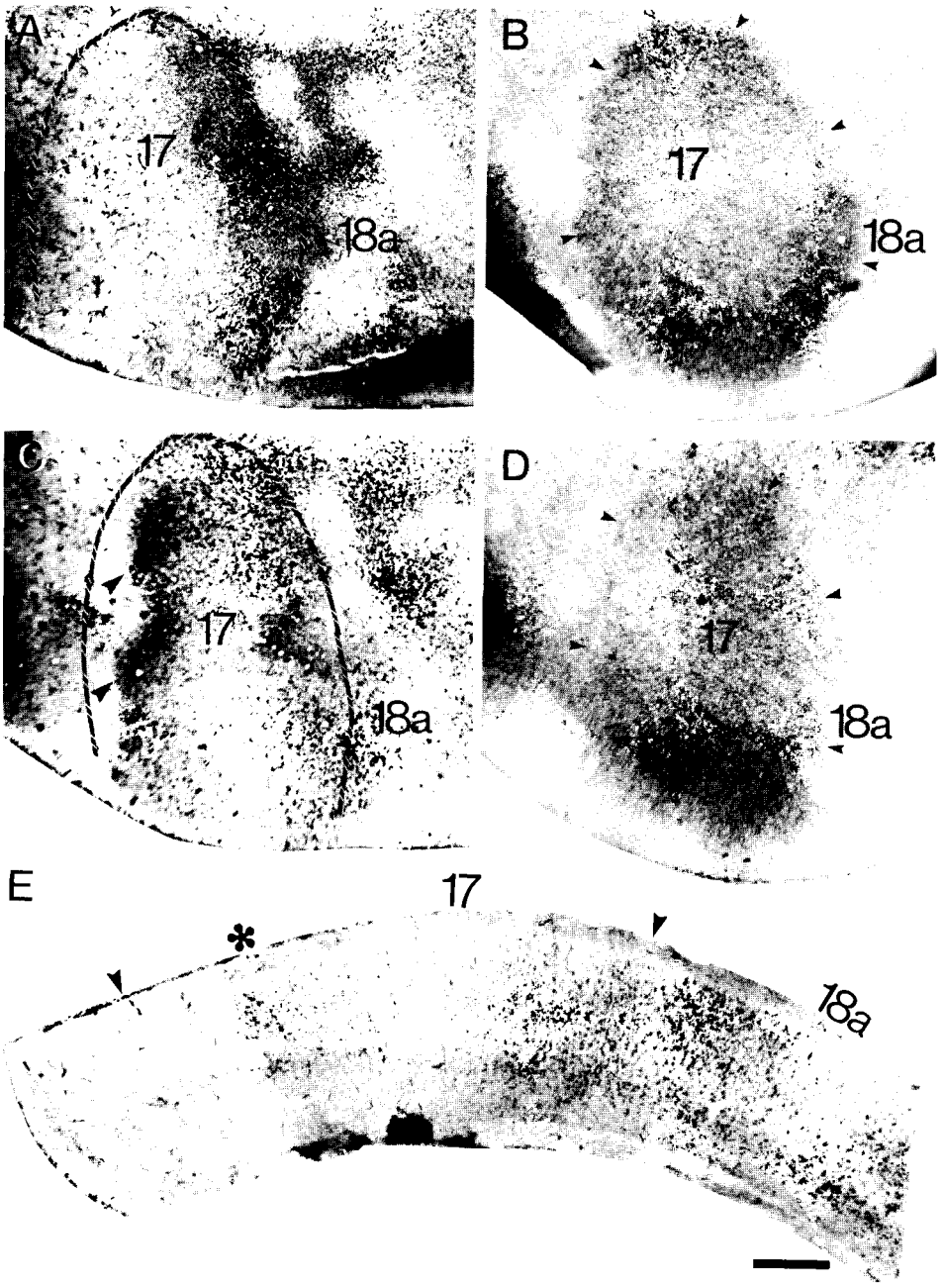

Fig 1. A-D. Visual callosal connections and myeloarchitecture in normally-reared (A,B) and monocularly enucleated (C,D) hamsters. Anterior is up, medial is to the left. **A.** Brightfield low-power photomicrograph of HRP-reacted tangential section through supragranular layers of hemisphere contralateral to the HRP injections. Dark areas are dense aggregates of retrogradely labeled perikarya and anterogradely labeled terminations. The dashed line indicates the border of area 17 drawn from an hematoxylin stained adjacent section (B) from same animal. **B.** Brightfield low-power photomicrograph of myelin-stained tissue section from same animal shown in A. Area 17 is the ovate, densely myelinated area in the posterior neocortex (arrowheads). **C.** Brightfield low-power view of HRP-reacted tangential section through supragranular layers of hemisphere ipsilateral to remaining eye in adult hamster monocularly enucleated at birth. Arrowheads indicate the anomalous bands of callosal labeling found within medial area 17. The dashed line in C indicates the border of area 17 drawn from the myeloarchitectonic pattern illustrated in D. **D.** Brightfield low-power view of myelin-stained tangential section through layer 4 of same hemisphere shown in C. **E.** Callosal connections in monocularly enucleated hamster studied in the coronal plane. Brightfield low-power photomicrograph of HRP-reacted section from hemisphere ipsilateral to remaining eye from an adult hamster monocularly enucleated at birth. Dorsal is up, medial is to the left. Arrowheads indicate the borders of area 17 determined from adjacent Nissl-stained sections. Asterisk indicates the anomalous column-like accumulation of HRP labeling in medial striate cortex. Scale bar = 1000 μm (A-D); 300 μm (E).

tions from HRP injected brains were reacted using the method of Mesulam (1978). Sections from Fluoro-Gold injected brains were mounted onto gelatin coated slides and analyzed under epifluorescence. In order to identify the borders of striate cortex (Caviness, 1975), alternate series of coronal sections were stained with cresyl violet while alternate series of tangential sections were stained with hematoxylin. As illustrated in Figure 1B, striate cortex in the hamster appears as a distinct ovate area of dark staining in myelin-stained tangential sections.

In order to quantify the effect of monocular enucleation on the distribution of callosal labeling in area 17, we performed a densitometric analysis of the callosal labeling in the hemisphere ipsilateral to the remaining eye in three monocularly enucleated hamsters. We also obtained the profile of callosal labeling density in one normally-reared rat for comparison. Photographic negatives of representative tangential sections from each animal were digitized using a Nikon Cool-Scan, and the data obtained were displayed and analyzed using the graphics program NIH Image. In each

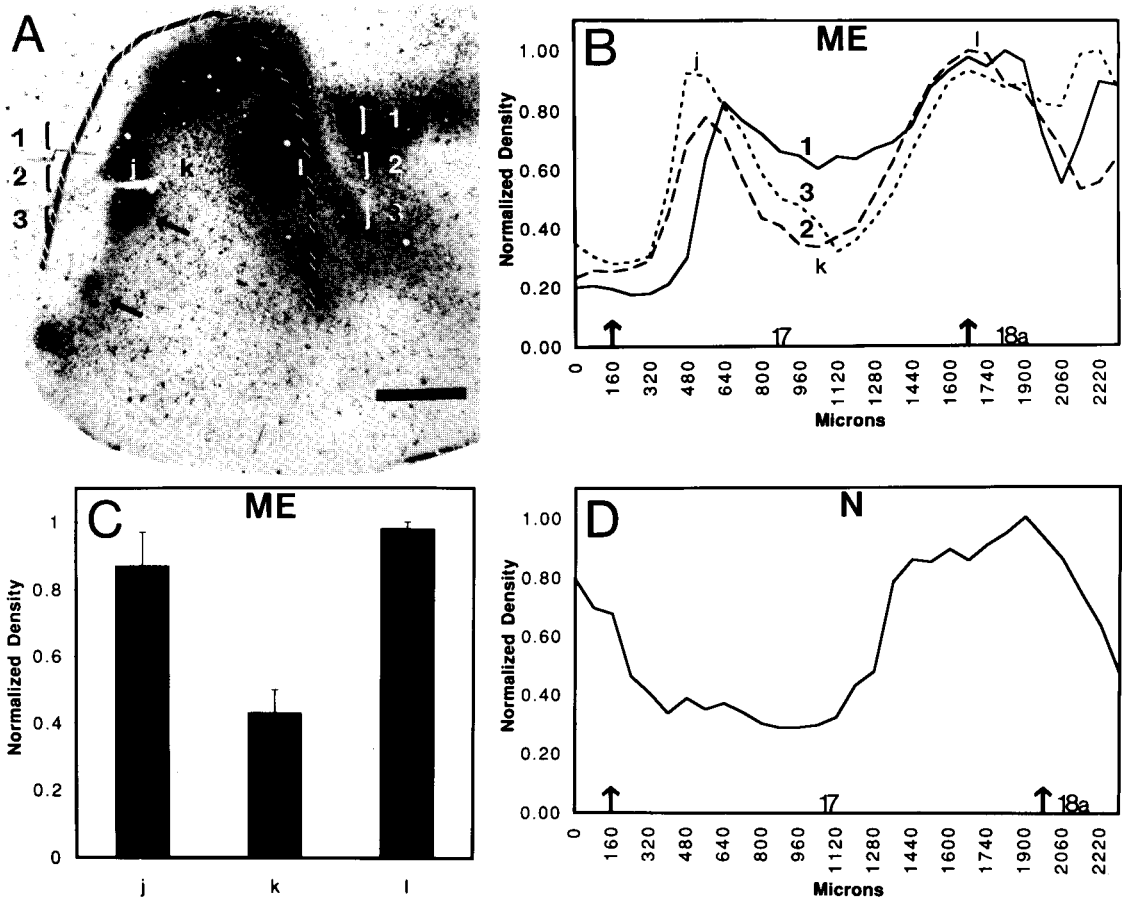

Fig 2. Densitometric analysis of HRP labeling across striate cortex of normally-reared and monocularly enucleated hamsters. **A.** Callosal pattern in hemisphere ipsilateral to the remaining eye in monocularly enucleated hamster. The dashed line indicates the border of area 17 determined from adjacent myelin-stained sections. Arrows indicate anomalous band of callosal labeling in medial striate cortex. Brackets labeled 1, 2 and 3 indicate areas analyzed densitometrically. Scale bar = 1000 μm. **B.** Densitometric curves 1, 2, and 3 come from areas indicated by brackets 1, 2 and 3 in A, respectively. The labeling density peaks located in medial area 17 are indicated by *j*, while the peaks located at the 17/18a border are indicated by *l*. In each tracing, the region of lowest density between peaks *j* and *l* is marked *k*. **C.** Histogram comparing the mean values obtained in regions *j*, *k* and *l* in the three monocularly enucleated hamsters analyzed. Vertical lines indicate SEM's. **D.** Densitometric curve from normally-reared hamster (case shown in Fig 1A). These data were obtained at an anteroposterior level similar to the level marked 2 in A. The increase in density values near the medial border of area 17 (arrow at 160 μm) is due to artifactual labeling resulting from diffusion of HRP from the contralateral hemisphere. All data have been normalized by dividing the density values by the highest value obtained in each scan.

section analyzed, the distribution of callosal labeling across the width of area 17 was measured at three antero-posterior levels (indicated by brackets in Fig 2A). The values obtained were normalized by dividing them by the highest value obtained in each scan.

RESULTS

Normally-reared hamsters

A major feature of the callosal pattern in normally-reared hamsters is a dense band of labeled cells and terminations located at the 17/18a border (Fig 1A). As seen in tangential section this band measures about 1 mm in width and appears homogeneously labeled, with relatively smooth borders. The border of area 17, indicated by a dashed line, was determined by superimposing the border of area 17 revealed in a neighboring tangential section stained for myelin (Fig 1B). In extrastriate cortex, densely labeled areas delineate at least three regions poor in callosal connections which appear to be closely related to subdivisions of extrastriate visual cortex described recently in this species (Olavarria and Montero, 1990). Our results from normally-reared hamsters are in good agreement with previous descriptions of the visual callosal pathway in this species (Dursteler *et al*, 1979; Rhoades and DellaCroce, 1980a; So and Jen, 1982; Olavarria and Montero, 1990).

Monocularly enucleated hamsters

We were particularly interested in studying the callosal pattern in the hemisphere ipsilateral to the remaining eye because an anomalous band of callosal connections develops in this hemisphere in one-eyed rats (Olavarria *et al,* 1987). The callosal pattern in the hemisphere contralateral to the remaining eye has been described as normal in appearance in rats (Olavarria *et al*, 1987), as well as in hamsters (Rhoades and DellaCroce 1980b). Thus, the data we analyzed came from animals that received tracer injections into the hemisphere contralateral to the remaining eye.

Figure 1C shows the overall callosal pattern in the hemisphere ipsilateral to the remaining eye in a monocularly enucleated hamster. The dashed line in Figure 1C represents the border of area 17 determined from an adjacent section stained for myelin (Fig 1D). Comparison of the data in Figure 1C with that in Figure 1A illustrates our finding that all major features of the pattern in normally-reared hamsters can be recognized in the pattern from monocularly enucleated hamsters, including the band of dense callosal labeling at the 17/18a border and the regions poor in callosal connections in lateral extrastriate cortex. However, an entirely new feature can also be seen in the pattern of one-eyed hamsters, namely, a dense band of labeling running rostro-caudally within medial area 17 (see arrowheads in Fig 1C). This band varies somewhat in medio-lateral position within area 17 from case to case, but in all animals studied it can be clearly distinguished from the 17/18a band, except at its rostral end, where it is confluent with the 17/18a band. The labeling pattern in the extra band commonly exhibits fluctuations in density, which gives the band a beaded appearance. We also observed an anomalous band of callosal connections in one-eyed hamsters injected with Fluoro-Gold, a fluorescent tracer that is preferentially transported in the retrograde direction (Schmued and Fallon, 1986). In all cases analyzed the labeling pattern was similar in all sections through supragranular layers.

Figure 1E shows the distribution of callosal connections in the hemisphere ipsilateral to the remaining eye in a monocularly enucleated hamster that was analyzed in the coronal plane. The arrowheads represent the borders of area 17 determined from adjacent sections stained with cresyl violet. As in normally-reared hamsters (data not shown, see also Rhoades and DellaCroce, 1980a), the band of labeling at the 17/18a border seen in coronal sections appears as a dense column of both anterograde and retrograde labeling extending virtually throughout the depth of the cortex. Under high power analysis the retrograde labeling was observed mainly in layers 2,3,5 and 6 whereas the anterograde labeling seemed to pervade all the cortical layers. However, unlike normally-reared hamsters, a second column of callosal labeling is present

in medial portions of area 17 (asterisk in Fig 1E). This second column of labeling can be readily distinguished from the 17/18a callosal band, and judging by its location relative to the 17/18a band and the borders of striate cortex, it most likely corresponds to the anomalous band of callosal connections observed in tangential sections (Fig 1C). In this band, the laminar distribution of callosal cells and terminations observed under high power was similar to that observed in the callosal band at the 17/18a border in normally-reared hamsters. Thus, callosal cells were predominantly found in laminae 2,3,5 and 6 with little labeling in the molecular and granular layers, while callosal terminations were found in all cortical laminae. Finally, scattered labeled cells were also observed between the two column-like bands in supragranular layers of striate cortex in monocularly enucleated hamsters.

Our densitometric analysis of the HRP-labeling across striate cortex (Fig 2) provided further evidence that the anomalous labeling in the hemisphere ipsilateral to the remaining eye was not homogeneously distributed in the direction parallel to the cortical surface. In order to facilitate the comparison across cases, the values of labeling density obtained in each scan were normalized by dividing them by the highest value obtained. As is illustrated in Figure 2A, data were collected at three anteroposterior levels (indicated by brackets), and Figure 2B shows the curves obtained at each level in this animal. These curves show that the distribution of callosal labeling in striate cortex of monocularly enucleated hamsters peaked in two regions (j and l) separated by a region of lower density (k). The peak (j) located in medial portions of area 17 probably corresponds to the anomalous band of callosal labeling observed in tangential sections (Fig 1C), while the lateral peak (l) most likely corresponds to the band of callosal labeling observed at the 17/18a border in tangential sections (Fig 1C). Figure 2C shows the average density values obtained at the locations *j*, *k* and *l* in three monocularly enucleated hamsters. A repeated measures analysis of variance (ANOVA) on these data indicated a significant difference between the average densities measured at these three locations ($F(2,6) = 52.0$, $p < 0.01$). Moreover, Tukey's HSD post hoc test showed that while peak labeling densities at locations *j* and *l* are not significantly different from each other, they were both significantly greater than the average density at location *k*. Figure 2D shows the profile of callosal labeling density obtained across area 17 in a normally-reared hamster (case shown in Fig 1A). These data were obtained at an anteroposterior level similar to the level marked 2 in Figure 2A. Comparison of Figures 2B and 2D indicates that the density peak *j* found in medial area 17 in monocularly enucleated hamsters is not observed in normal hamsters.

DISCUSSION

A prominent anomaly induced by the removal of one eye at birth in hamsters is the appearance of a band of callosal connections in medial striate cortex ipsilateral to the remaining eye. The labeling at the 17/18a border and in lateral extrastriate cortex is not obviously different from the labeling in the corresponding regions in normally-reared hamsters. In addition, no marked changes in the laminar distribution of callosal connections were observed, suggesting that the development of the tangential and radial distributions of callosal connections are under the guidance of different mechanisms (Olavarria *et al*, 1987).

Comparison of our present results with those presented by Olavarria *et al* (1987) in one-eyed rats reveals that neonatal enucleation induces the development of a remarkably similar anomaly in the callosal patterns of rats and hamsters. Moreover, our data suggest that the abnormal callosal band in hamsters is located somewhat closer to the medial border of striate cortex than in one-eyed rats. These findings demonstrate that the rat is not the only species capable of developing novel callosal features in response to neonatal enucleation, and they suggest that this capability may be common among rodents. Furthermore, the high degree of similarity of the callosal anomalies in rats and hamsters suggests that the eyes' influence on the development of the visual callosal pathway is similar in both rodent species.

Although our results bear some similarities with previous studies of visual callosal connections in enucleated hamsters, they also differ in important ways. Rhoades and DellaCroce (1980b) studied the distribution of callosal connections in monocularly enucleated hamsters and reported that the main effect observed in the hemisphere ipsilateral to the remaining eye was a marked increase in width of the column-like accumulation of callosal connections near the 17/18a border. These authors do not specifically mention an extra band of callosal connections within striate cortex. The differences between these previous studies and the present one may be due, at least in part, to differences in sectioning techniques. While we have used tangential sections to study the overall distribution of callosal connections, Rhoades and DellaCroce used mainly coronal sections, which are generally less effective for revealing fine details of patterns in the direction parallel to the brain surface.

Specification of the callosal pattern

The differences between our results and those from Rhoades and DellaCroce (1980b) merit attention because they suggest different roles for the eye in the development of visual callosal pathways. A widespread distribution of callosal connections is compatible with the notion that disruption of visual input arrests the developmental process that shapes the mature distribution of callosal cells (Rhoades and DellaCroce, 1980b; Rothblat and Hayes, 1982; Murphy and Grigonis, 1988; but see Fish *et al*, 1991). However, this mechanism alone appears insufficient to explain the emergence of discontinuous features in the callosal pattern, such as the extra callosal band described in monocularly enucleated rats (Olavarria *et al*, 1987) and hamsters (present study).

In both rats (Lund *et al*, 1973; Manford *et al*, 1984; Jeffery, 1984; Reese, 1986) and hamsters (So *et al*, 1984) removal of one eye at birth leads to the development of an exuberant retino-thalamo-cortical projection ipsilateral to the remaining eye. It has been argued (Olavarria *et al*, 1987) that anomalies in the retinotopic map represented in this abnormally expanded ipsilateral ascending pathway induce the development of the anomalous band of callosal connections in striate cortex of one-eyed rats. More specifically, since the callosal connections in areas 17 and 18a of the rat normally concentrate along representations of the central visual field (Thomas and Espinoza, 1987), it was suggested that the location of the extra callosal band corresponds to an aberrant representation of the central visual field in middle portions of striate cortex. The more medial location of the extra callosal band in one-eyed hamsters compared to one-eyed rats may be a reflection of differences in the topography represented in the anomalous ipsilateral retinofugal projections in these species.

Evidence in support of these ideas comes from studies in rats (Fukuda *et al*, 1984; 1985; Jeffery and Thompson, 1986), and in hamsters (Thompson, 1979; Finlay *et al*, 1979; Rhoades, 1980), indicating that removal of one eye increases the complexity of the retinotopic organization conveyed by the ipsilateral retino-tectal projection. Of particular relevance for the present study are the reports by Thompson (1979) and Jeffery and Thompson (1986) that, in the hamster, the colliculus ipsilateral to the remaining eye contains two retinotopic maps of the visual field along the rostrocaudal axis.

More recent studies of the visual pathway further support the idea that abnormalities in the callosal pattern correlate with irregularities in the topography of the dorsal lateral geniculate nucleus (dLGN) and striate cortex. In one-eyed hamsters, Trevelyan and Thompson (1992) used anatomical methods to map the geniculo-cortical projection in the hemisphere ipsilateral to the remaining eye and found that the visual cortex receives two sets of projections from the dLGN, one mirroring the other. In one-eyed rats, correlation of callosal labeling with electrophysiological mapping data indicates that the map in striate cortex presents marked anomalies that often include an over-representation of central portions of the field in the region of the extra callosal band (Ruthazer *et al*, 1993).

Thus, the anomalies in the retinotopic organization that were first recognized in the

retinotectal projections of one-eyed rats and hamsters appear to be similar to the anomalies relayed to the striate cortex via the retino-geniculo-cortical pathway. Although the actual process by which the eyes influence callosal development is not yet fully understood, it appears likely that this abnormal retinotopic information contributes to the development of the discontinuous anomalous features observed in the callosal patterns of one-eyed rats and hamsters.

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