

Regeneration of an abnormal ipsilateral visuotectal projection in *Xenopus* is delayed by the presence of optic fibres from the other eye

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SUMMARY

Optic fibre regeneration was studied by [³H]proline autoradiography and by mapping electrophysiologically the direct visuotectal projections to the contralateral and ipsilateral tecta 12–16 weeks after sectioning the right optic nerve in *Xenopus* two to four weeks after metamorphosis. The experiments were carried out in three groups: (A) optic nerve section in newly metamorphosed animals with embryonic left-eye enucleation; (B) optic nerve section with simultaneous left-eye enucleation; and (C) optic nerve section with delayed left-eye enucleation 5–31 days prior to sacrifice.

In all but three animals regenerated optic fibres were demonstrated morphologically both in the contralateral and ipsilateral tecta. The contralateral visuotectal projection was fully restored within the 12–16 weeks in all animals. In animals with embryonic enucleation or in those where the enucleation was carried out simultaneously with optic nerve section, a direct ipsilateral visuotectal projection was established at the same time as the restoration of the contralateral projection. In contrast, no direct ipsilateral visuotectal projection was detectable in the presence of optic fibres from the other eye in the doubly innervated tecta. However, 14–31 days after the removal of the incumbent optic fibres by left-eye enucleation a direct visuotectal projection from the right eye to the ipsilateral tectum was established, and its polarity corresponded to the normal contralateral retinotectal projection.

The apparent disparity between morphological and electrophysiological findings in the doubly innervated tectum suggests that superimposed optic fibres are unable to form normal synaptic relations with tectal neurons during early regeneration, delaying the establishment of the induced direct ipsilateral visuotectal projection.

INTRODUCTION

The retinotectal projection in frogs is entirely crossed, with the optic axons terminating in retinotopic order in the superficial tectal neuropil. Besides the direct contralateral projection of the retina/visual field to the tectum, an indirect ipsilateral visuotectal projection, subserving binocular vision, has also been reported (Gaze & Jacobson, 1962). This indirect ipsilateral pathway involves a polysynaptic intertectal linkage relayed through the isthmus nucleus (Gruberg &

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Udin, 1978). Thus, in normal animals tectal points receive a direct contralateral and an indirect ipsilateral retinal input.

Following optic nerve section regeneration occurs and optic fibres re-establish their normal retinotopic representation on the tectum in frogs (Sperry, 1944). Electrophysiological studies of long-term optic nerve regeneration in frog have shown that in some animals, in addition to the restoration of the contralateral retinotectal projection, regenerating axons may project abnormally to the ipsilateral tectum (Gaze & Jacobson, 1963; Gaze & Keating, 1970). The abnormal direct ipsilateral visuotectal projections in these studies partly or completely overlapped the normal contralateral projection from the other eye. Since the retinotectal projection after optic nerve section was not assessed morphologically, these authors were unable to establish whether the absence of abnormal ipsilateral visuotectal projection in many animals was due to the inability to detect the presence of optic fibres electrophysiologically or to the failure of bilateral fibre growth in the majority of animals. In a recent study in young *Xenopus* using both morphological and electrophysiological methods we have shown, with [^3H]-proline ($^3\text{H-P}$) autoradiography, that following optic nerve section regenerated optic fibres usually innervated both the contralateral and ipsilateral tecta (Glastonbury & Straznicky, 1978). In contrast, electrophysiological mapping of the regenerated optic fibre projection in the same animals indicated that whilst the contralateral projection was restored, the ipsilateral projection observed by $^3\text{H-P}$ autoradiography was undetectable electrophysiologically. A similar finding has been reported on the aberrant ipsilateral retinotectal projection in *Rana pipiens* using behavioural tests (Misantone & Stelzner, 1974). After unilateral enucleation and tectal removal an abnormal ipsilateral retinotectal projection was induced, with a resultant mirror-image misdirection of striking reflexes in the visual field. The onset of mirror-image striking behaviour through the aberrant ipsilateral retinotectal projection was delayed or even prevented in the presence of incumbent optic fibres from the other eye.

The apparent disparity between morphological and electrophysiological results during the early phase of optic nerve regeneration in the doubly innervated ipsilateral tectum is intriguing and invites further investigation. It is conceivable that the synaptic arrangement of the frog tectum (Székely, 1973) makes it difficult for regenerated optic fibres to induce new postsynaptic sites or to displace incumbent optic fibres from postsynaptic sites, delaying the formation of connexions between aberrant optic fibres and tectal neurons. Optic fibres which fail to establish normal synaptic contacts may branch diffusely over the tectum and consequently they may generate insufficient electric field to be detectable electrophysiologically. It is possible but less likely that aberrant optic fibres establish normal connexions with tectal neurons but are rendered inactive through interaction with optic fibres from the other eye. Experiments on fish and urodele muscles suggest that inappropriate synapses from foreign nerves may be sup-

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pressed by fibres of the appropriate motor nerve normally innervating the muscle (Mark, 1980).

This study has been undertaken to elucidate whether the inability to detect an ipsilateral direct visuotectal projection during early regeneration is due to delayed formation of a normally ordered retinotectal projection, followed presumably by the establishment of the normal synaptic relations, or to transient functional repression of aberrant optic fibres. This report shows that the direct ipsilateral retinotectal projection only becomes detectable electrophysiologically about two to four weeks after the elimination of incumbent optic fibres, thus furnishing support for the first alternative.

MATERIALS AND METHODS

Xenopus laevis, the clawed frog, was used in this study.

Surgery. In the first group of animals, under MS 222 (Tricaine Methane Sulphonate, Sandoz) anaesthesia (1:5000 solution) the left eye in 25 embryos was enucleated at stages 31–32 (Nieuwkoop & Faber, 1956). Two to four weeks after metamorphosis, under MS 222 (1:1500 solution) anaesthesia the optic nerve was exposed through the pharynx and cut close to the ventrolateral wall of the brain. In the second group of animals, the right optic nerve was exposed and cut close to the chiasma two to four weeks after metamorphosis; at the same time the left eye was enucleated. In the third group of animals the right optic nerve was cut two to four weeks after metamorphosis and 10, 11, 12 and 13 weeks later the left eye was enucleated. All animals were raised to metamorphosis and beyond under standard conditions (Straznicky, 1976). The operated animals in the three groups were kept separately and were used for autoradiographic and electrophysiological studies 12–16 weeks after optic nerve section.

Electrophysiology. The method of mapping the visuotectal projections was similar to that previously described (Straznicky, Gaze & Keating, 1971). For recording purposes, platinum-tipped lacquer-insulated tungsten or Wood's metal microelectrodes were used with tip diameters of 1–2 μm or 10–15 μm and impedances of 2–5 megohm and 0.1 megohm respectively. Animals were anaesthetized with intraperitoneal injections of 0.4 ml MS 222 (0.2%) and immobilized with turbocurarine (0.2 mg intramuscularly). The tectum was exposed, single or multi-unit action potentials were recorded from terminal arborizations of optic fibres at pre-determined tectal positions, and the corresponding receptive fields were mapped. Maps were based on recordings from about 30 different tectal positions on each side in each animal.

Histology. Twenty-four hours before visuotectal mapping and subsequent sacrifice 10 μCi [^3H]proline isotope (specific activity 24 Ci/mmol, Amersham) in 0.5 μl solution was injected into the posterior chamber of the right eye. After recording, the head of each animal was fixed in Bouin's fixative, the dissected brain embedded in paraffin and later serially sectioned at 10 μm . The closely

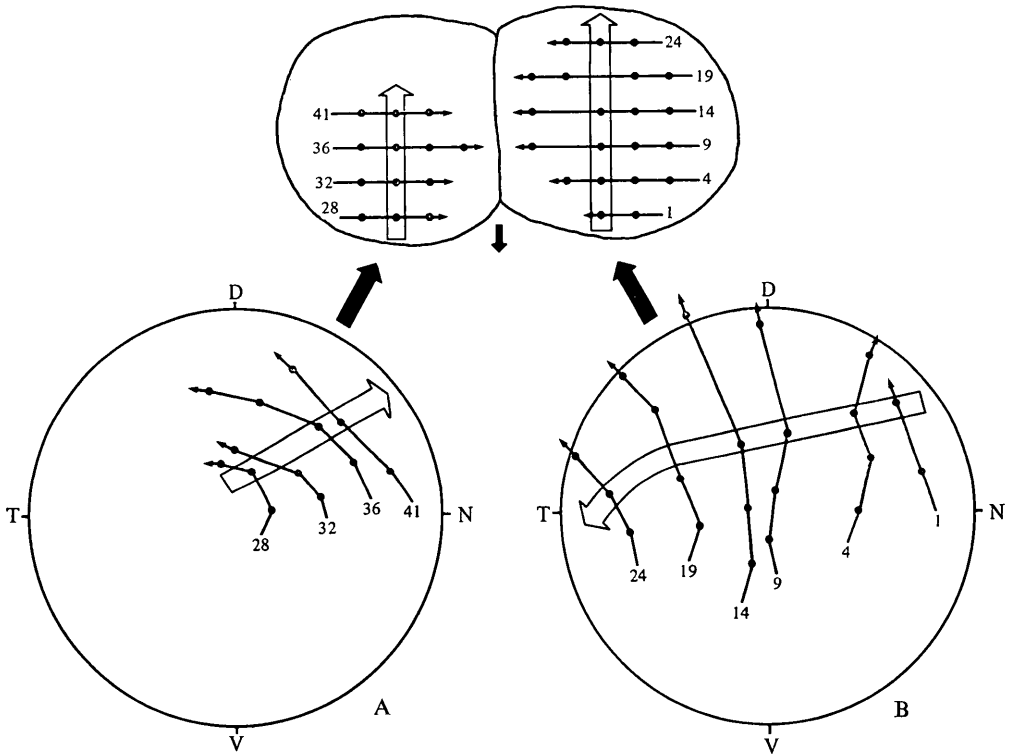


Fig. 1. Visuotectal projections from the right eye in normal *Xenopus*. The small black arrow shows the rostral tectal direction. The visual field charts are centred on the optic axis of the eye, extending out 100° radially. D, dorsal; V, ventral; T, temporal and N, nasal. The numbered rows of stimulus positions in the field correspond to the rows of tectal positions. The large open arrows indicate the orientation of the visual field in relation to the open arrow on the tectum. (A) Indirect ipsilateral projection from right eye to right tectum. Note that the nasotemporal polarity of the ipsilateral visuotectal projection is reversed with respect to that of the contralateral visuotectal projection. (B) Contralateral projection from right eye to left tectum. The nasotemporal polarity of the visual field matches up with the rostrocaudal tectal axis.

spaced sections were coated with K2 nuclear emulsion (Ilford), exposed at 4°C for 14 days, developed in Kodak Dektol and then counterstained with Harris's haematoxylin. The optic fibre regeneration to the contralateral and ipsilateral tecta was assessed semi-quantitatively on the basis of the autoradiographic silver grain density, measured in reflected light, in the superficial tectal layer (Glastonbury & Straznicky, 1978; Straznicky, Gaze & Horder, 1979).

RESULTS

Bilateral tectal innervation from the regenerated right optic nerve was demonstrated by $^3\text{H-P}$ autoradiography in 33 of the 36 animals in this study. The aberrant retinotectal projection separated from the main contralateral projec-

Table 1. Retinotectal and visuotectal projections in the control and three experimental groups of animals

Group	Retinotectal projections		Visuotectal projections	
	Contralateral	Ipsilateral	Contralateral	Ipsilateral
A (9)	9	6	9	5
B (8)	8	8	8	8*
C (14)†	14	12	14	5
Cc (5)	5	5	5	—

* One animal in this group had partially established ipsilateral visuotectal projections.

† Details of the results from this group of animals are given in Table 2. The number of animals used in each group is in brackets. A = optic nerve regeneration following embryonic enucleation. B = optic nerve regeneration with simultaneous unilateral enucleation. C = optic nerve regeneration with subsequent enucleation. Cc = optic nerve regeneration without enucleation.

tion at the chiasma, and from there fibres travelled along the margin of the diencephalon to the pretectal area and finally to the ipsilateral tectum. Both contralateral and ipsilateral optic fibre projections were distributed in the superficial optic fibre receiving layer of the tectum (Fig. 2).

The pattern of the normal visuotectal projection in *Xenopus*, for comparison with those mapped electrophysiologically following optic nerve regeneration, is shown in Fig. 1. In the contralateral visuotectal projection the nasal field projects to the rostral and the temporal field to the caudal part of the tectum (Fig. 1B). Thus the nasotemporal polarity of the visual field projection is represented rostrocaudally on the tectum. In addition to the contralateral projection there is an indirect ipsilateral projection from the same eye. This indirect ipsilateral projection, however, differs from the direct contralateral projection in two respects: namely (1) the polarity of the nasotemporal axis in relation to the contralateral projection is reversed (Figs 1A and B); and (2) evoked action potentials to visual stimulations, through the indirect ipsilateral projection, are generated with about 20–30 msec delay. On the basis of these two differences direct and indirect visuotectal projections can be distinguished.

A. Optic nerve regeneration following embryonic enucleation

³H-P autoradiography showed bilateral regrowth of regenerating optic fibres in six animals and only contralateral innervation in the three remaining animals of this group (Table 1). Of the six animals exhibiting bilateral regrowth, in five the silver grains were distributed across the whole extent of the tectum, indicating fairly even tectal innervation by aberrant optic fibres, whilst in one animal the ipsilateral projection was very sparse and was confined to the rostral part of the tectum. Since the ipsilateral tectum had not received direct optic fibre inputs prior to the arrival of regenerating optic fibres, the superficial layer of the tectum

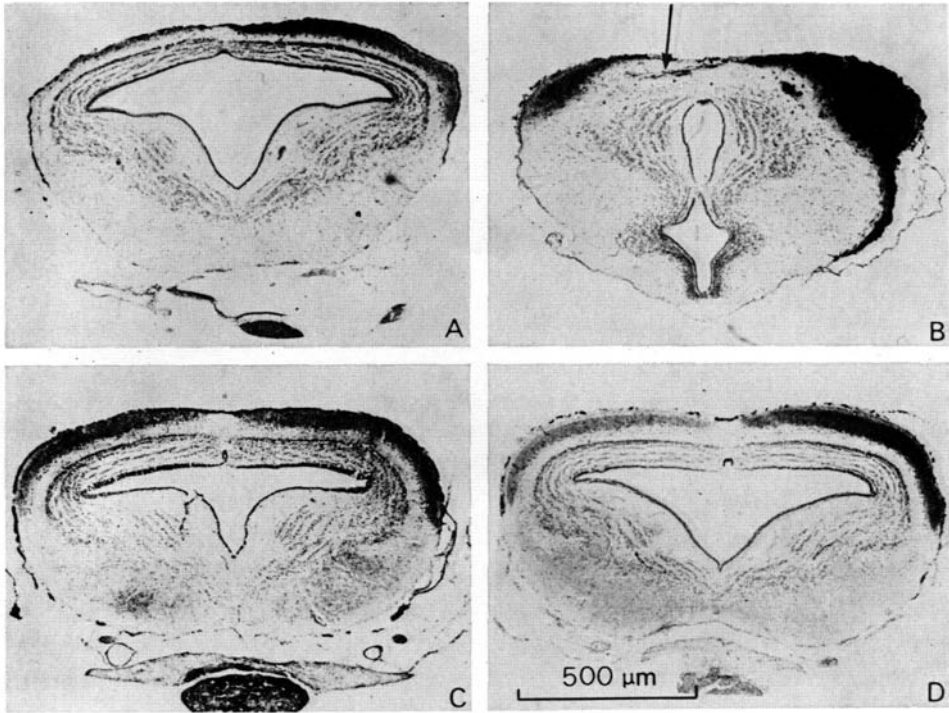


Fig. 2. Bright field photographs of [^3H]proline autoradiographs of the contralateral (right side of each picture) and ipsilateral (left side of each picture) tecta from the right eye. Scale is the same in each photograph. Bar in D represents 500 μm . (A) Animal with embryonic left eye enucleation. (B) Animal with embryonic left eye enucleation. Arrow points at the pretectal commissure through which regenerated optic fibres enter the ipsilateral tectum. (C) Animal with right optic nerve section and simultaneous left eye enucleation. (D) Animal no. 13 with left eye removal 30 days before sacrifice. The visuotectal recordings of this animal appear on Figs 4 and 5.

which received optic fibres was thinner than in the normal or in the contralateral side of the same animal (Fig. 2A). An unexpected finding was that in two animals optic fibres entered the ipsilateral tectum through a completely abnormal pathway, from the contralateral pretectal area via the pretectal commissure to the ipsilateral tectum (Fig. 2B).

Electrophysiological mapping showed that the visuotectal projection to the contralateral side was fully restored in eight out of the nine animals in this group while only partly restored visuotectal projection was observed in the remaining animal (Table 1). In four animals, in addition to the contralateral projection, a retinotopically organized direct visuotectal projection was also found in the ipsilateral tectum (Fig. 3). Of the remaining two animals with autoradiographically confirmed ipsilateral projection, one showed a poorly organized visuotectal projection to the ipsilateral tectum. In the other animals no projection to the ipsilateral tectum could be established electrophysiologically.

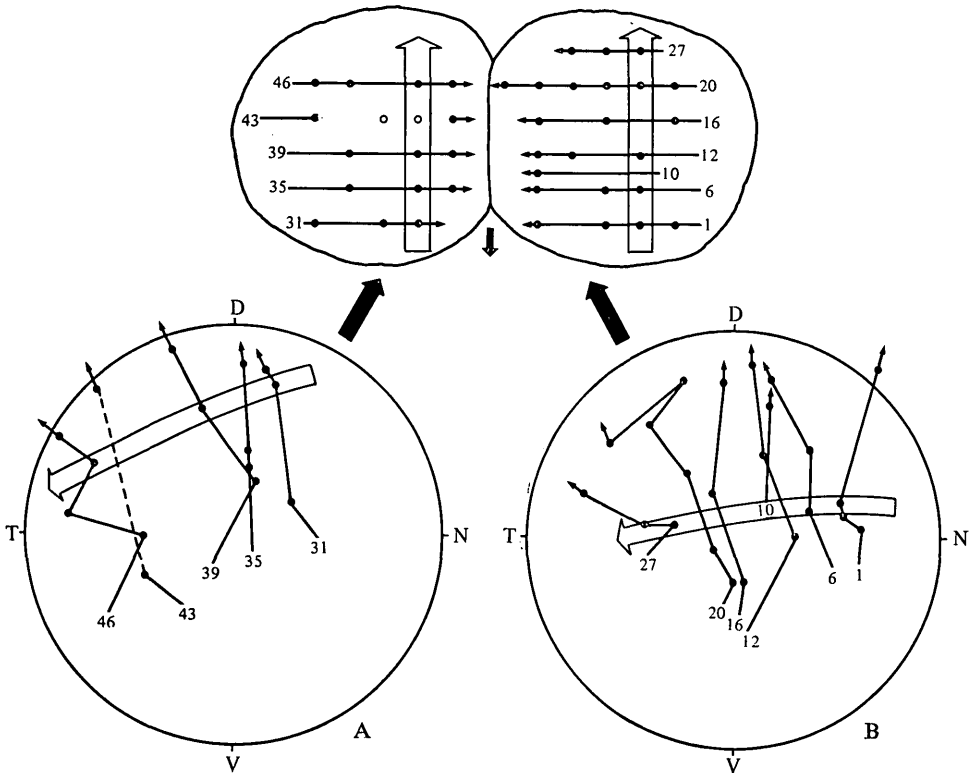


Fig. 3. Visuotectal projections after optic nerve regeneration to the contralateral (B) and ipsilateral (A) tecta in an animal with embryonic eye enucleation. Note that direct and orderly visuotectal projections have been re-established on both contralateral and ipsilateral tecta.

B. Optic nerve regeneration with simultaneous unilateral enucleation

³H-P autoradiography in the eight animals of this group confirmed that optic fibres regenerated to both contralateral and ipsilateral tecta (Fig. 2C). In seven animals the electrophysiological mapping showed a good direct visuotectal projection across both tecta (Table 1). In the remaining animal a partial and disorganized projection was found and this was restricted to the rostral half of the ipsilateral tectum. The autoradiography on this animal confirmed that the regeneration to the ipsilateral side was poor.

C. Optic nerve regeneration with subsequent enucleation

The left eyes of fourteen animals belonging to this group were enucleated 5–31 days prior to electrophysiological mapping and sacrifice (Table 2). Both contralateral and ipsilateral regenerations were demonstrated in all nineteen animals by ³H-P autoradiography. Electrophysiological mapping showed that the contralateral visuotectal projections were restored in all cases within the 12–16 weeks

Table 2. *Retinotectal and visuotectal projections following right optic nerve section in animals with delayed left eye enucleation*

Animal no.	Survival time after optic nerve section	Survival time after eye enucleation	Retinotectal projection		Visuotectal projection	
			Contralateral	Ipsilateral	Contralateral	Ipsilateral
1	13W	1W	++	+	Restored	—
2	14W	5D	++	++	Restored	—
3	13W	1W	+++	++	Restored	—
4	13W	6D	+++	++	Restored	Few points only
5	14W	2W	+++	+	Restored	Few points only
6	14W	2W	+++	+++	Restored	—
7	13W	12D	+	++	Partly restored	Partly restored
8	15W	20D	+++	++	Restored	Few points only
9*	First recording	5D			Restored	—
	Second recording	3W	+++	++	Not recorded	Partly restored
10	13W	23D	++	—	Restored	—
11*	First recording	8D			Partly restored	Few points only
	Second recording	4W	++	++	Partly restored	Partly restored
12	16W	4W	++	—	Restored	Few points† only
13*	First recording	1W			Restored	Few points only
	Second recording	30D	+++	++	Not recorded	Restored
14	14W	31D	+++	++	Restored	Restored

The silver grain density of the normal optic fibre projection is marked ***, about two-thirds or one-third of the normal silver grain density is marked ** and * respectively. Poor optic fibre regeneration to the ipsilateral tectum and the resultant sparseness or absence of silver grain density is marked — which also designates the lack of detectable visuotectal projection.

W = weeks, D = days, * = two subsequent recordings performed, † = presumably indirect ipsilateral responses.

survival time after optic nerve section. Despite the successful bilateral optic fibre regeneration, no visuotectal projections were recorded from the ipsilateral tectum in the five control animals where the left eye had not been enucleated (Table 1). This observation is in full agreement with our previous finding on the inability to record the ipsilateral visuotectal projection of the aberrant optic fibres in the presence of incumbent optic fibres from the other eye (Glastonbury & Straznicky, 1978). Of four animals where electrophysiological recordings were made shortly (5–14 days) after the enucleation of the left eye, two had only a few visually

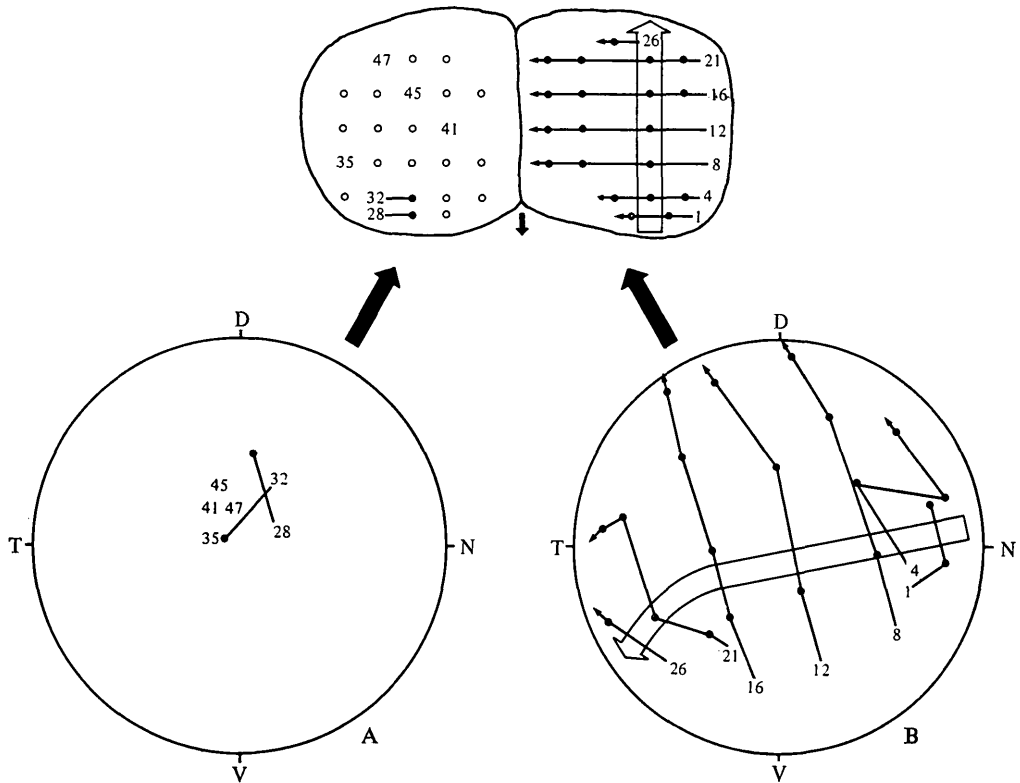


Fig. 4. Contralateral (B) and ipsilateral (A) visuotectal projections in animal no. 13 at the time of the first recording one week after left eye enucleation. In contrast to the well-established contralateral projection, only a few visual responses were obtained from the ipsilateral tectum.

evoked responses. In these animals it was not possible to determine whether the responses came through the direct or indirect ipsilateral visuotectal projection. The third animal had a partial ipsilateral visuotectal projection. The fourth animal did not have a recordable ipsilateral visuotectal projection, though the presence of aberrant ipsilateral retinal fibres was established with $^3\text{H-P}$ autoradiography.

Seven animals were recorded electrophysiologically and sacrificed 20–31 days after enucleation. Five of them had partly or fully developed direct ipsilateral visuotectal projections. In three animals (9, 11 and 13) we succeeded in carrying out electrophysiological mapping twice, one week after enucleation and a second time two to three weeks after the first recordings (Table 2). In all three animals the second recording revealed substantial improvement in the direct ipsilateral projection. The typical case of these animals is shown in Figs 4 and 5. At the time of the first mapping session only a few visual field points were recorded from the ipsilateral tectum (Fig. 4A). In contrast, three weeks later the direct ipsilateral

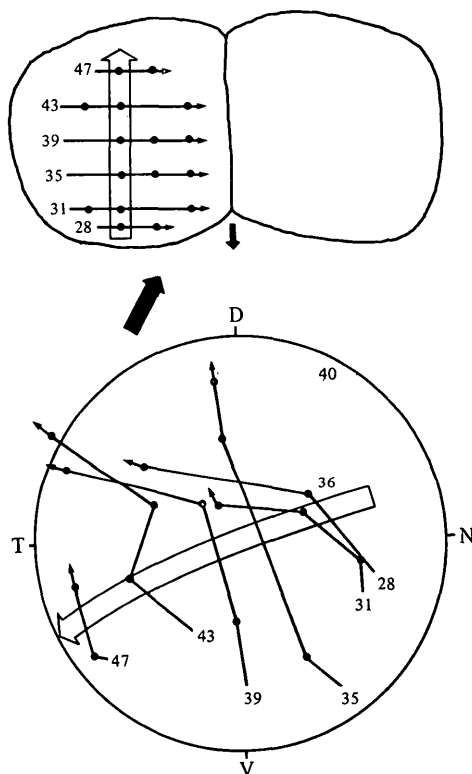


Fig. 5. Direct ipsilateral visuotectal projection in animal no. 13, recorded 30 days after left eye enucleation and 23 days after the first mapping (see Fig. 4). The contralateral projection was not mapped during the second recording session. Note that the ipsilateral visuotectal projection recovered completely during the time elapsed between the first and second recordings.

projection was completely established, comparable to the contralateral projection (Fig. 5). Autoradiography on these animals revealed successful regeneration to both contralateral and ipsilateral tecta (Fig. 2D).

Electrophysiological mapping of these animals was carried out using both, or only one, of the high- and low-tip-impedance electrodes. Since there was no noticeable difference between the visuotectal maps obtained by either tungsten or Wood's metal electrodes in the same animal, it appeared as if the ease of recording of ipsilateral responses in these animals did not depend on the type of electrode used but on the length of time that had elapsed after enucleation.

DISCUSSION

In a former paper we have shown that, following optic nerve section, regenerating optic fibres regularly innervate both contralateral and ipsilateral tecta in *Xenopus* and that a substantial part of the optic fibre projection terminates in

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the ipsilateral tectum (Glastonbury & Straznicky, 1978). We have also shown that no electrophysiological responses are recorded from these fibres. The present study shows that about 12 weeks is sufficient to re-establish a visuotectal projection in the contralateral tectum. In all but a few animals the contralateral visuotectal projections were comparable to the nasotemporal and dorsoventral organization of the normal projection. Gaze & Jacobson (1963) have reported successful optic nerve regeneration in adult *Rana temporaria*, though in a large number of their animals the contralateral visuotectal projection failed to return to normal even one year after optic nerve section. In many of the animals in their study, disorganized or partly organized visuotectal projections persisted. The high rate of successful regeneration and the subsequent restoration of the orderly visuotectal projections in this report may be due to the better regeneration of young post-metamorphic frogs.

The present series of experiments shows apparent differences in the ease of inducing electrophysiologically recordable direct ipsilateral projections in the absence or presence of optic fibres from the other eye. Following either embryonic eye removal or enucleation carried out simultaneously with optic nerve section, morphological retinotectal as well as direct electrophysiological visuotectal projections were established in the ipsilateral tectum at approximately the same time as the contralateral visuotectal projection reappeared. It has been shown by Feldman, Gaze & Keating (1971) that a normal visuotectal projection is readily restored on a 'virgin' tectum which had not received optic fibre input up to the time of the arrival of regenerating retinal fibres. Their observations and our results suggest that the time of entry of optic fibres into the tectum is not critical for the formation of an orderly retinotectal projection. The incidence of bilateral optic nerve regeneration after embryonic enucleation was lower than in animals with both eyes present. In an earlier experiment we have shown that a millipore filter barrier, implanted into the chiasma, did not prevent fibres crossing to the contralateral side (Straznicky *et al.* 1971). While the contralateral growth tendency of optic fibres is quite apparent during regeneration, optic fibres also readily follow the intact optic pathway from the other eye through the chiasma to the ipsilateral tectum. Contact guidance of regenerating fibres such as that provided by the intact optic pathway is not available in animals with embryonic enucleation. In two animals with embryonic enucleation an ipsilateral retinotectal projection was formed via the pretectal commissure. It has been shown that after larval unilateral tectal ablation some of the optic fibres grow to the remaining tectum via the posterior and pretectal commissures (Straznicky & Glastonbury, 1979). It appears that commissural pathways are available for optic fibres as an alternative route to the ipsilateral tectum after metamorphosis, at the time when the development of the brain and the formation of the commissures has been completed.

Our observations demonstrate that after short periods of regeneration (12–16 weeks) no visually evoked responses can be recorded electrophysiologically

from the superimposed aberrant optic fibre projection. Since the ipsilateral direct visuotectal projection becomes established very slowly, i.e. about two to four weeks after the removal of the incumbent optic fibres, it seems unlikely that these ipsilateral fibres, after having made synaptic contact with tectal cells, were functionally repressed because of interactions between the incumbent and superimposed optic fibres. The long delay experienced would appear to indicate that the ipsilateral fibres form normal synaptic relations only on vacated tectal cells following the removal of the incumbent fibres. The two to four weeks period may represent either a slow establishment of normal synaptic relations or a delay due to the persistence of degenerating contralateral axons after enucleation. Both assumptions are compatible with recent ultrastructural studies on the restoration of the retinotectal synaptic relationships (Östberg & Norden, 1979).

The ipsilateral direct projection which appears after enucleation corresponds to the normal contralateral projection on the basis of its polarity and of the short delay in evoking the visual responses. That is, we are dealing with two direct retinal projections, one to the contralateral and one to the ipsilateral tectum, and not with an indirect ipsilateral projection which may also recover after section of one optic nerve (Keating & Gaze, 1970). It has been demonstrated that superimposed optic fibres eventually establish functional connexions in a doubly innervated tectum (Gaze & Jacobson, 1963; Gaze & Keating, 1970; Misantone & Stelzner, 1974). It is thus likely that these fibres compete successfully for synaptic sites with incumbent fibres, but the process leading to the formation of a superimposed retinotectal connexion is very slow. The present results on short-term optic nerve regeneration permit us to assume that either (1) the formation of synapses of superimposed optic fibres is delayed, or (2) if they are formed, these terminals are not large enough or suitably arranged so as to generate a recordable extracellular electric field. Since visuotectal mapping involves recording evoked potentials from presynaptic terminals (Gaze, 1970), neither the applied electrophysiological nor the anatomical (³H-P autoradiography) approaches enable us to choose between the two possible alternatives. Further ultrastructural studies are in progress in this laboratory to elucidate this problem.

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