J. Physiol. (1976), 257, *pp.* 621–643
With 1 *plate and* 8 *text-figures*
Printed in Great Britain

PROGRESS OF TOPOGRAPHIC REGULATION OF THE VISUAL PROJECTION IN THE HALVED OPTIC TECTUM OF ADULT GOLDFISH

BY MYONG G. YOON
From the Department of Psychology, Life Sciences Centre, Dalhousie University, Halifax, Nova Scotia, Canada

(*Received 19 August 1975*)

SUMMARY

1. The patterns of re-established visual projections on to the rostral half-tectum are studied following excision of the caudal tectum at various intervals after section of either the contralateral optic nerve or the ipsilateral optic tract in adult goldfish.

2. The pattern of a newly restored retinotectal projection depends on the duration of the post-operative period given to the halved tectum before it is re-innervated by regenerating optic fibres from the retina.

3. When the duration is such that regenerating optic fibres invade the denervated rostral half-tectum at about 40 days or longer after excision of the caudal tectum, the remaining half-tectum is able to accommodate incoming optic fibres not only from the appropriate temporal hemiretina but also from the foreign nasal hemiretina in an orderly compressed topographic pattern.

4. If the surgical operations are timed so that the halved tectum receive regenerating optic fibres earlier than 33 days after excision of the caudal tectum, the halved tectum initially accommodates only those optic fibres originating from the temporal half of the retina at this early stage.

5. This normal (uncompressed) pattern of the newly regenerated visual projection, however, eventually changes into an orderly compressed pattern at a later period. Post-operative dark-deprivation of the operated fish has no significant effect on the temporal transition.

6. The temporal transition from an initially normal pattern into an orderly compressed pattern may reflect the time course of progressive and systematic changes involved in topographic regulation of the halved tectum into a whole.

INTRODUCTION

The pattern of visual projections from the retina on to the mid-brain optic tectum is organized in a specific topographical order. In a normal goldfish, the nasal half of the visual field projects to the rostral half of the contralateral tectum and the temporal half of the field projects to the caudal half of the tectum. Thus a nasotemporal sequence in the visual field is represented by a rostrocaudal sequence on the tectum, and a dorsoventral series in the field by a mediolateral series on the tectum.

When the original neural connexions between the retina and the tectum are interrupted by severing the optic fibres in an adult goldfish, the proximal parts of the severed axons of the retinal ganglion cells are able to regenerate, and eventually restore the visual projections in correct topographic order: the tangled regenerating optic fibres somehow unsort themselves, preferentially select particular routes to their respective destinations, and then make functional re-connexions with predesignated target zones in the tectum. (For review see Sperry, 1965; Gaze, 1970; Jacobson, 1970; Hunt & Jacobson, 1974; Crossland, Cowan, Rogers & Kelly, 1974; Meyer & Sperry, 1974.)

The visual system of an adult goldfish is also capable of re-adjusting to various types of experimentally induced size disparity between the retina and the optic tectum (Gaze & Sharma, 1970; Yoon, 1971, 1972*a*, *b*, 1975*a*; Sharma, 1972*a*, *b*). About 4 months after removal of the caudal half of the tectum in adult goldfish, Gaze & Sharma (1970) observed an orderly compression of visual projections from the entire range of the contralateral visual field on to the remaining rostral half-tectum (which previously received projections from only the nasal half of the visual field). Furthermore the compression of retinotectal projection was found to be a reversible phenomenon in adult goldfish (Yoon, 1972*a*): the visual projections from the whole retina become compressed on to the rostral half of the tectum following surgical insertion of a mechanical barrier between the intactly innervated rostral half and the denervated caudal half of the tectum. When the barrier is either removed or absorbed later, the field compression disappears, and a normal pattern of visual projections from the retina on to the whole extent of the re-joined tectum is restored. If the caudal half of the same tectum is excised, the remaining rostral half-tectum reacquires the visual projections from the whole retina in an orderly compressed topographic pattern.

How soon does the field compression on to the rostral half-tectum occur following excision of the caudal half? The present experiments on adult goldfish show that it takes at least a month for the halved tectum to be able to accommodate regenerating optic fibres not only from the temporal hemiretina but also from the foreign nasal hemiretina in an orderly compressed form. When the regenerating optic fibres re-innervate the rostral half-tectum at an earlier post-operative period, the fish shows no sign of a field compression in the newly restored visual projection. Only the nasal half of the visual field projects to the remaining rostral half-tectum at this early stage. A preliminary account of the results was presented elsewhere (Yoon, 1975*b*).

METHODS

Goldfish (*Carassius auratus*) used in the present experiments weighed about 10–15 g and were about 65–75 mm from the nose to the base of the tail at the time of surgery. Individual fish were anaesthetized by immersion in 0·03 % ethyl-*m*-aminobenzonate methane sulphonate (MS 222, Sandoz) for 2–5 min, and then placed between two wet sponge pads in a holder that restrained the fish in a desired position for surgery or neurophysiological recording. The gills were continually infused with aerated water at a rate of about 0·5 l. per minute through a tube in the mouth.

The optic tectum was exposed by opening a single cranial bone flap that was restored at the completion of surgery or neurophysiological recording, or both. The experiments involved various combinations of the following types of surgical manipulations: complete section of the optic nerve at a distance of about 0·5–1 mm from the posterior pole of the eyeball (see Pl. 1*F*); excision of the entire caudal half of the optic tectum (Pl. 1*B*); complete section of the optic tract at a position just before it bifurcates into the medial branch (which innervates the dorsomedial area of the ipsilateral tectum) and the lateral branch (which innervates the curled ventrolateral area of the same tectum) as shown in Pl. 1*D* and *E*. In order to expose the optic tract, emerging from the optic chiasm beneath the two fore-brains, the posterior part of the ipsilateral forebrain was either displaced or removed (Pl. 1*C*, *D* and *E*).

The operated fish in a dark-deprived group were kept in transparent glass aquaria that were continually illuminated with incandescent lamps throughout the experimental period. An average luminance of these aquaria was about 20 ft. lamberts. The other operated fish were kept under a regular daily cycle of 12 hr light and 12 hr darkness. The mean water temperature was about 22° C.

Standard neurophysiological methods were used for mapping retinotectal projections as described in previous reports (Yoon, 1971, 1975*a*, *d*). In brief, action potentials, elicited or modulated by visual stimuli, were recorded from the deep tectal layers by advancing tungsten micro-electrodes at a depth between 150 and 300 μm. The locations of the recording micro-electrodes on the dorsal surface of the tectum were marked on polaroid photographs of the tectum at 21–33 × magnifications. The corresponding receptive fields for the visual units were marked on the perimetric chart of the contralateral visual field. The cornea of the fish's eye, exposed in the air, was continually bathed with a uniform flow of water infused from the tip of a fine cannula. In some cases, the extra-ocular muscles were cut to immobilize the eyeball.

RESULTS

Retinotectal projections following excision of the caudal tectum at various intervals after section of the contralateral optic nerve

Following section of the optic nerve near the posterior pole of the eyeball in adult goldfish, the proximal residues of the severed axons regenerate back to the tectum. As will be shown in Experiments 1 and 2, it takes 43–53 days following the optic nerve section for the ingrowing optic fibres to establish a visual projection in the tectum. Suppose that surgical operations are timed so that regenerating optic fibres invade the denervated rostral half-tectum at various predesignated intervals after excision of the caudal half of the tectum. Would the topographic pattern of the newly re-established visual projections on to the remaining half-tectum depend on the duration of post-operative period allowed to the halved tectum before it is re-innervated by incoming optic fibres?

Experiment 1

In seventy-two goldfish, the right optic nerve was sectioned near the posterior pole of the right eyeball. The surgery was performed in all seventy-two fish within 16 hr. The experimental fish were kept in a regular cycle of 12 hr in light and 12 hr in darkness.

The caudal half of the denervated left tectum was excised in thirteen groups of experimental fish at different intervals ($\Delta\tau$): 0, 5, 8, 12, 16, 19, 22, 25, 28, 31, 35, 38 and 42 days after section of the right optic

---

Text-fig. 1. Diagrammatic summary of the patterns of re-established visual projections on to the rostral half of the left tectum following excision of the caudal tectum at various intervals after section of the right optic nerve. The right optic nerve was sectioned near the posterior pole of the right eyeball in all experimental fish on the same day (the 0th day). The operated fish were kept in a regular daily cycle of 12 hr in light and 12 hr in darkness. The double bar (—| |—) indicates the date on which the caudal half of the denervated left tectum was excised at various intervals (denoted by $\Delta\tau$ in days) after section of the optic nerve. Each fish is represented by one horizontal figure. The dashed line with a vertical bar at its right end (------|) indicates that the fish did not give any visual responses from the left tectum on the testing date. The horizontal bar with an arrow at its right end (➔) indicates that the projection from the whole right visual field was found to be compressed on to the remaining rostral half of the left tectum in the fish on the date of the mapping experiment. The continuous horizontal line with an open square at its right end (——□) indicates that the fish showed a normal (uncompressed) projection from the nasal half of the visual field on to the rostral half-tectum on the testing date. In several cases, consecutive maps were obtained from the same experimental fish at different post-operative periods.

nerve as shown in Text-fig. 1. Four fish were operated on in each group, except the last group ($\Delta\tau = 42$ days), which had only three fish. Before tectal surgery, the whole left tectum was checked for any sign of re-innervation in each fish by neurophysiological recording methods. Only those fish which did not give any visual responses from the left tectum

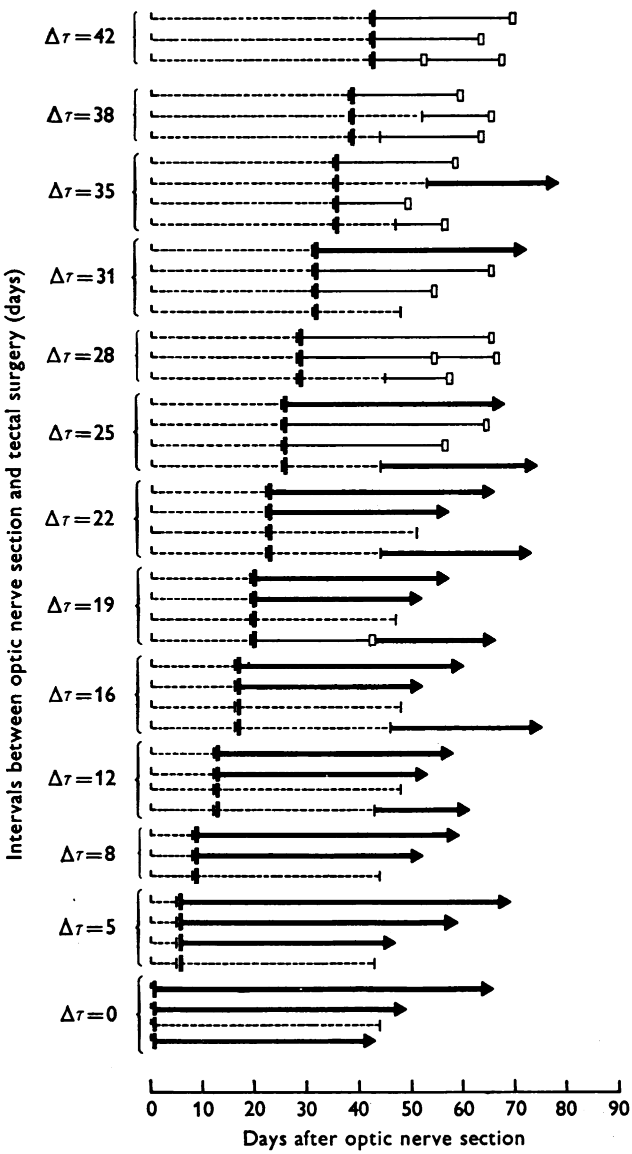


Fig. 1. For legend see facing page.

received the surgical operation of the caudal tectum immediately after the test. Two of six fish, tested 38 days, and four of seven fish, tested 42 days after section of the optic nerve, gave vague, sporadic visual responses within a small area near the rostral pole of the left tectum. These six fish were excluded from the experiment. No further tectal surgery was performed after the group $\Delta\tau = 42$ days.

Neurophysiological mapping experiments began for a total of fifty-one operated fish (out of the seventy-two fish). Three fish died prematurely. Patterns of re-established retinotectal projections were mapped for the other forty-eight fish at various periods between 43 and 78 days after section of the right optic nerve. The results obtained from the forty-eight experimental fish are summarized in Text-fig. 1. In seventeen fish, tested at periods between 43 and 53 days after section of the optic nerve, the remaining rostral half-tectum gave either no visual responses at all, or a few sporadic responses which were too vague to map their receptive fields. Nine of the seventeen fish were tested again at later post-operative periods. Re-innervations eventually occurred in these fish, and retinotectal projection maps were obtained from all nine fish.

Two types of topographic patterns were observed in the newly re-established visual projections from the right retina on to the remaining rostral half of the left tectum. In twenty-four cases, mapped at periods between 33 and 66 days after excision of the caudal tectum, the newly re-established visual projections showed a field compression (denoted by ➔ in Text-fig. 1): the entire range of the right visual field projected on to the remaining rostral half of the left tectum in correct retinoptic order (for example, see Text-fig. 8*A*). On the other hand, nineteen fish showed a normal, uncompressed pattern (denoted by ——□ in Text-fig. 1) in their newly restored visual projections which were mapped at earlier periods between 11 and 40 days after excision of the caudal tectum: only the nasal half of the right visual field projected on to the remaining rostral half of the left tectum (for example see Text-fig. 7).

One should emphasize the fact that the initially uncompressed, normal pattern of newly re-established visual projection is transitory: it eventually changes into a compressed pattern as the post-operative period progresses. An example of the temporal transition is shown by one fish in group $\Delta\tau = 19$ days. This fish showed a normal, uncompressed pattern in the newly restored visual projection, mapped 24 days after excision of the caudal tectum. When the same fish was tested again 23 days later, not only the nasal half but also the temporal half of the visual field projected on to the remaining rostral half-tectum in an orderly compressed form. The temporal transition from an initially uncompressed state into a compressed state of re-established retinotectal projections complicated the results of the foregoing time series experiments. Would it be possible to delay or even suppress this temporal transition?

Experiment 2

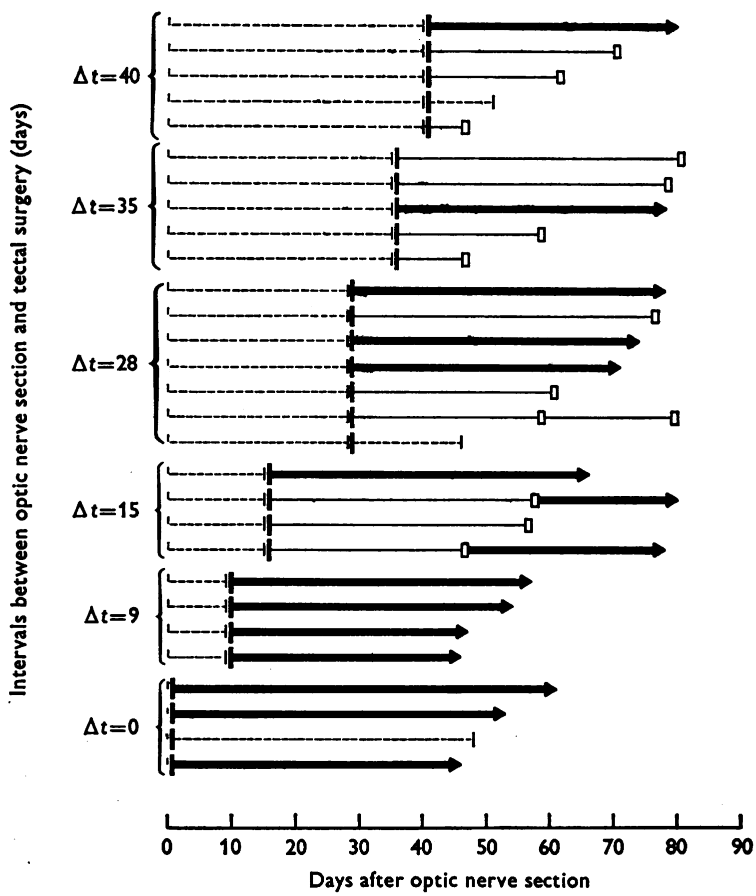
A previous study (Yoon, 1975*a*) showed that post-operative dark-deprivation of operated goldfish somehow delayed the field compression following excision of the caudal half of the tectum, if the original connexions between the temporal half of the retina and the remaining rostral half-tectum were left intact. Would continual inputs of visual stimuli help those optic fibres regenerated from the temporal hemiretina to retain their newly formed connexions with the remaining rostral half-tectum in an initially normal, uncompressed pattern?

In thirty-six goldfish, the right optic nerve was sectioned near the posterior pole of the right eyeball. The surgery was performed in all thirty-six fish within a day. These fish were continually exposed to visual stimuli without any dark period (post-operative dark-deprivation). The caudal half of the denervated left tectum was excised in six groups of the dark-deprived fish at different intervals (Δt), 0, 9, 15, 28, 35, and 40 days after section of the right optic nerve following the same procedures as in Experiment 1. A total of thirty-one (out of the thirty-six) dark-deprived fish received the surgical operation of the caudal tectum. Two operated fish died prematurely. Retinotectal projections were mapped for the other twenty-nine experimental fish at various periods between 46 and 81 days after section of the optic nerve.

The results obtained from the twenty-nine dark deprived fish are summarized in Text-fig. 2. Three fish, tested 46, 48, and 51 days after section of the optic nerve showed no sign of re-innervation. A field compression was observed in fifteen cases, when their re-established retinotectal projections were mapped at post-operative periods between 37 and 65 days after excision of the caudal tectum. In fourteen other cases, however, the newly re-established visual projection showed a normal, uncompressed pattern, when they were mapped at earlier post-operative periods between 7 and 52 days after excision of the caudal tectum.

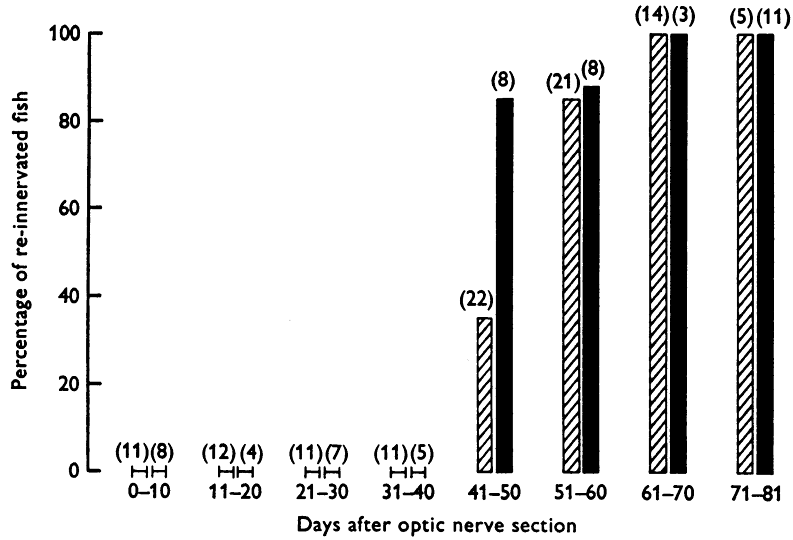
In spite of the continual dark-deprivation, the temporal transition from an initially uncompressed pattern into a compressed pattern occurred in two fish (see the group Δt = 15 days in Text-fig. 2). One of these dark-deprived fish showed a normal, uncompressed pattern in the newly restored visual projection, mapped 32 days after excision of the caudal tectum. When the same fish was tested again 31 days later, the visual projection became orderly compressed. The same temporal transition was also found in the other fish: its initially uncompressed pattern, mapped 43 days after the tectal surgery, changed into a compressed pattern when the visual projection in the same dark-deprived fish was re-mapped 22 days later.

How long did it take for regenerating optic fibres to re-innervate the rostral half-tectum after section of the optic nerve, under the conditions of Experiments 1 and 2? Text-fig. 3 shows a time histogram of the



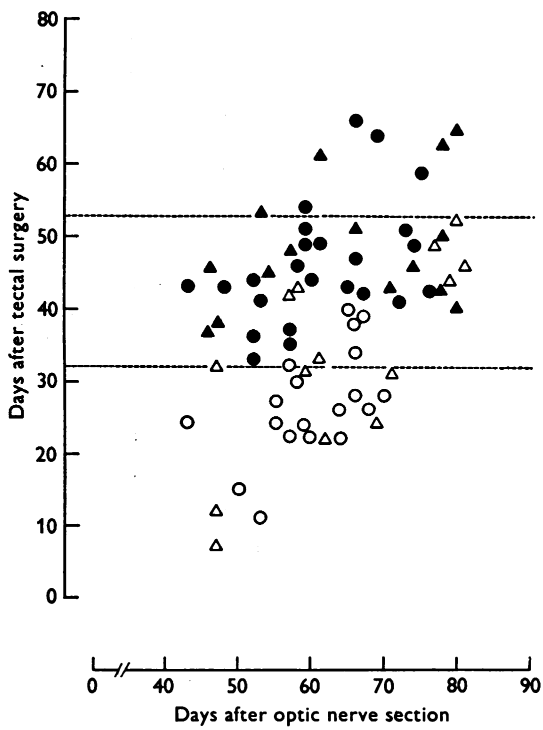
Text-fig. 2. Patterns of re-established retinotectal projections under post-operative dark-deprivation. Visual projections on to the rostral half of the left tectum were mapped at various post-operative periods following excision of the caudal tectum at different intervals (Δt in days) after section of the right optic nerve. The optic nerve was sectioned near the posterior pole of the eyeball in all fish on the same day (the 0th day). These operated fish were continually exposed to visual stimuli during the entire experimental periods. For denotation of symbols used in the diagram, see the legend of Text-fig. 1.

percentage of experimental fish which gave visual responses from the half-tectum. The stippled bars represent the results of Experiment 1, and those of Experiment 2 are shown by the filled bars in Text-fig. 3. In both experiments, the percentage of re-innervated fish increased rapidly as the post-operative periods progressed from 43 to 53 days after section of the optic nerve. All fish tested after 54 days completed re-innervation. In two fish, re-innervation occurred as early as 43 days after the optic nerve section.



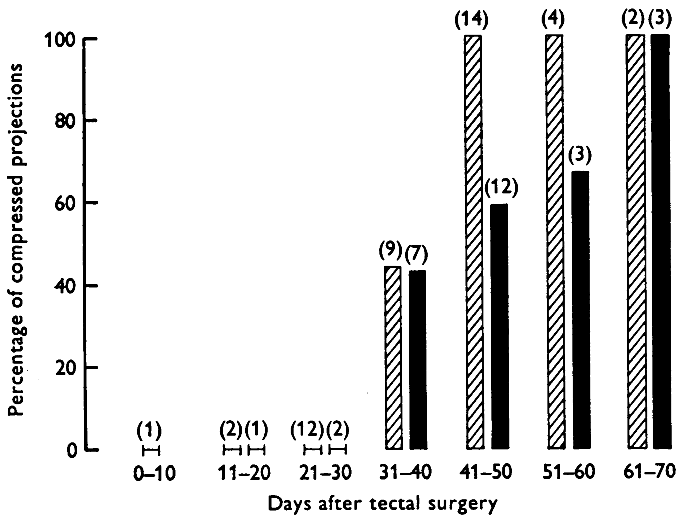
Text-fig. 3. Time histogram of the percentage of re-innervated fish. A total of seventy-seven fish were distributed into nine groups according to the period between the date of their mapping experiments and the date of the right optic nerve section (on the 0th day). Each group represents a period of 10 days. The vertical axis indicates the percentage of those fish which gave visual responses from the halved left tectum in each group. The hatched bars represent the results obtained in Experiment 1. The filled bars show the results obtained from the dark-deprived fish in Experiment 2. The number in parentheses indicates the total number of experimental fish on which a percentage is based for each group represented by a bar.

How long did it take to induce a field compression in the halved tectum under the conditions of Experiments 1 and 2? Text-fig. 4 shows a scatter diagram for the patterns of re-established retinotectal projections. The horizontal axis indicates the date of mapping experiments after section of the optic nerve on the 0th day. The vertical axis indicates the duration of post-operative periods between the date of tectal surgery and the date of mapping experiments. A compressed pattern is represented either by a filled circle (●) for those fish in Experiment 1 or by a filled triangle (▲) for the dark-deprived fish in Experiment 2. A normal (uncompressed) pattern is denoted either by an open circle (○) for those fish in Experiment 1 or by an open triangle (△) for the dark-deprived fish in Experiment 2. The scatter diagram shows an interesting fact: the patterns of newly re-established visual projection on to the halved tectum depend on the duration of post-operative periods between the date of tectal surgery and the date of the mapping experiment. Note that the



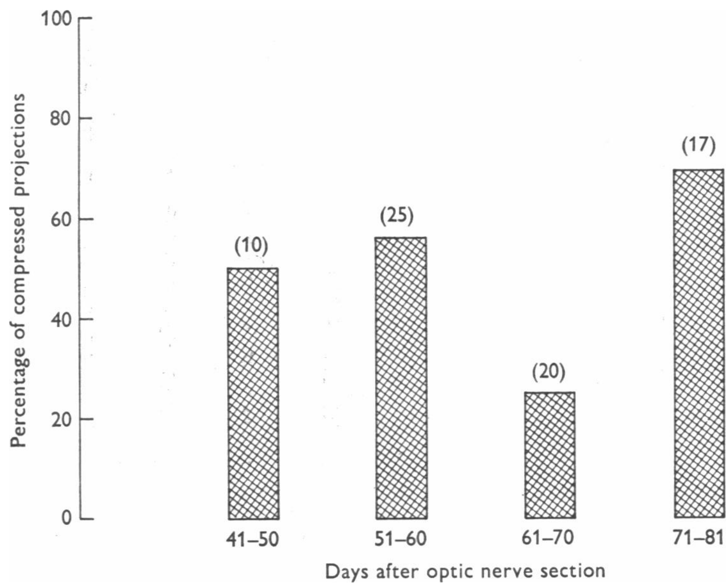
Text-fig. 4. Distribution of the patterns of re-established retinotectal projections in a scatter diagram. The horizontal axis indicates the date of the mapping experiment after section of the right optic nerve on the 0th day. The vertical axis indicates the duration of the post-operative periods between the date of excision of the caudal tectum and the date of the mapping experiments. A filled circle (●) represents a compressed pattern, and an open circle (○) indicates a normal (uncompressed) pattern observed in those fish tested in Experiment 1. A filled triangle (▲) shows a compressed pattern, and an open triangle (△) shows a normal pattern observed in the dark-deprived fish of Experiment 2. All fish below the horizontal dashed line at 32 days after tectal surgery showed a normal pattern, whereas those above the dashed horizontal line at 53 days showed a compressed pattern.

compressed patterns are dominant in the region of longer post-operative periods over 40 days after the tectal surgery, whereas normal (uncompressed) patterns appear predominantly in the region of shorter post-operative periods below 40 days. This trend becomes more evident in a time histogram as shown in Text-fig. 5. The vertical axis indicates the percentage of experimental fish which showed a field compression in their reconnected visual projections. The hatched bars represent the results obtained in Experiment 1 and the filled bars represent the results



Text-fig. 5. Time histogram of the percentage of the compressed pattern in the re-established retinotectal projections. A total of seventy-two maps were distributed into seven groups according to the duration of the post-operative periods between the date of tectal surgery and the date of the mapping experiments. Each group represents a duration of 10 days. The vertical axis indicates the percentage of those fish which showed a field compression in their re-established visual projection on to the rostral half-tectum, in each group. The hatched bars represent the results obtained in Experiment 1. The filled bars show the results obtained from the dark deprived fish in Experiment 2. The number in parentheses indicates the total number of experimental fish on which a percentage is based for each group represented by a bar.

obtained from the dark-deprived fish in Experiment 2. Note that none of the twenty-two fish tested between 7 and 32 days after the tectal surgery in both experiments showed any sign of a field compression in their newly restored visual projections. On the other hand, all of the twenty fish tested at post-operative periods longer than 41 days after the tectal surgery in Experiment 1 showed compressed patterns. In between these two extreme distributions, the percentage of compressed cases increased as the duration of post-operative periods increased. Note that the rate of increase in the percentage of compressed patterns was slower for the dark-deprived fish in Experiment 2 than for those fish under a normal visual environment in Experiment 1. This may reflect a very weak effect of the post-operative dark-deprivation in slowing down the temporal transition from an initially uncompressed pattern into a compressed one, during the longer post-operative periods between 41 and 53 days after the tectal surgery.



Text-fig. 6. Time histogram of the percentage of compressed patterns plotted according to the date of the mapping experiments after section of the optic nerve. The same seventy-two maps were distributed into four groups according to the periods between the date of the mapping experiments and the date of the optic nerve section on the 0th day. The vertical axis indicates the percentage of the tested fish (both in Experiments 1 and 2) which showed a field compression in their restored retinotectal projections. The number in parentheses indicates the total number of experimental fish on which a percentage is based for each group represented by a bar.

The scatter diagram shown in Text-fig. 4 reveals another interesting fact: the patterns of re-established visual projection on to the halved tectum do not directly depend on the post-operative periods between the date of optic nerve section (the 0th day) and the date of the mapping experiment. The latter trend becomes more explicit in a time histogram shown in Text-fig. 6. The vertical axis of the time histogram indicates the percentage of experimental fish (tested in Experiments 1 and 2) which showed compressed patterns in their re-established visual projections. A compressed pattern was observed as early as 43 days after the optic nerve section. This was also the earliest date on which visual responses were recorded from the previously denervated left tectum. During the early experimental periods between 43 and 50 days after section of the optic nerve, five fish showed a compressed pattern, while the other five fish showed a normal, uncompressed pattern in their newly re-established visual projections. Note that the percentage of compressed cases did not change in any significant way throughout the entire experimental period between 43 and 81 days after section of the optic nerve. Therefore, the pattern of a regenerated visual projection on to a halved tectum depended not on the time given to the regenerated optic fibres after their initial re-innervation of the halved tectum but on the post-operative period given to the halved tectum following excision of the caudal half.

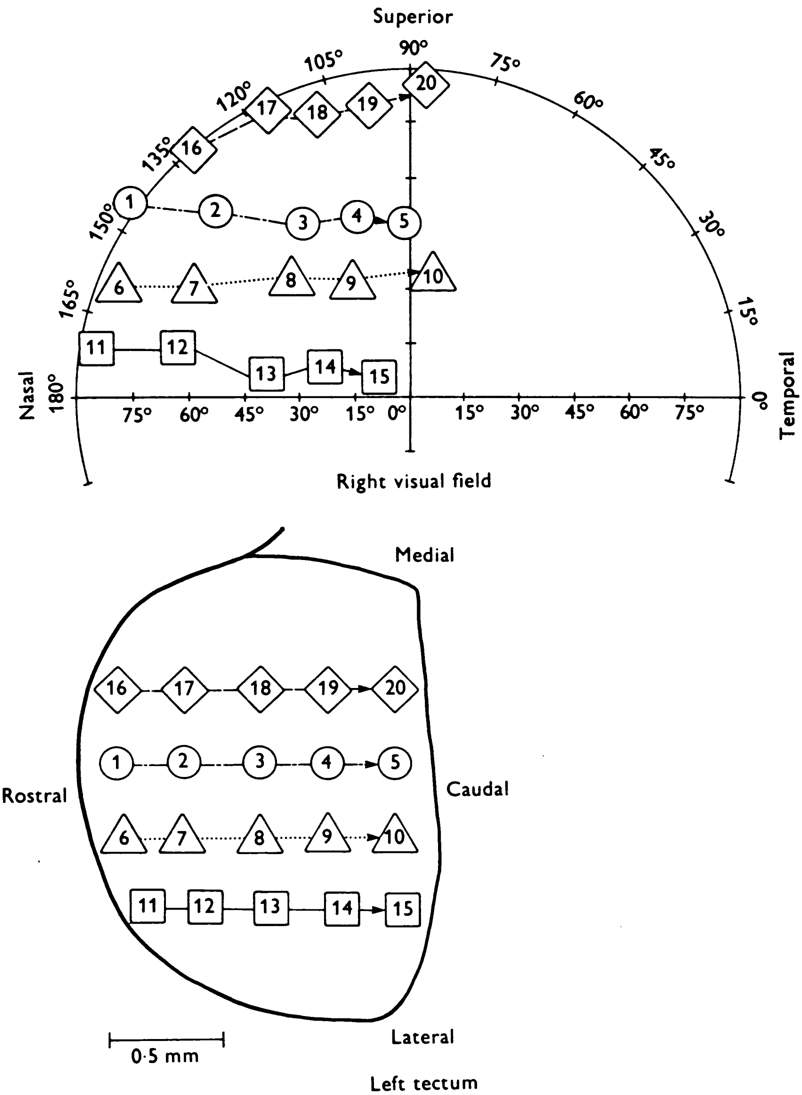
The results of Experiments 1 and 2 suggest that it takes at least a month of post-operative period (following excision of the caudal tectum) for a halved tectum to be able to accommodate regenerating optic fibres from the whole retina. When the incoming optic fibres re-innervated the halved tectum later than 40 days after the tectal surgery, a majority of the operated fish showed an initially compressed pattern in their newly re-established retinotectal projections. On the other hand, when the halved tectum received incoming optic fibres earlier than 33 days following the tectal surgery, all of the operated fish retained a normal, uncompressed pattern in their re-established visual projections, regardless of when they were mapped during the experimental period between 43 and 71 days after section of the optic nerve.

Retinotectal projections following excision of the caudal tectum and section of the ipsilateral optic tract

The experimental procedures used in the preceding Experiments 1 and 2 need further control tests to exclude the following possibilities: suppose that regenerating optic fibres invaded the denervated whole tectum relatively soon (say within 15 days after section of the optic nerve) but they had a long latent period (about 30 days) within the tectum, during which one could not record visual responses from these newly regenerated optic fibres. If so, the uncompressed state of the newly restored retinotectal projection should be regarded as an experimental artifact rather than a reflexion of the intrinsic property of the halved tectum itself.

Experiment 3

In twelve goldfish, the mid-brain was exposed (Pl. 1*A*), and then the caudal halves of both the right and the left tecta were excised (see Pl. 1*B*). Immediately after the tectal surgery, the left optic tract (which contained the axons of ganglion cells in the right retina) was sectioned near its entrance to the rostral end of the left tectum (see Pl. 1*C*, *D* and *E*). The



Text-fig 7. For legend see facing page.

remaining rostral half of the right tectum was also denervated by severing the left optic nerve near the posterior pole of the left eyeball (see Pl. 1*F*). The operated fish were kept under a regular daily cycle of 12 hr in light and 12 hr in darkness.

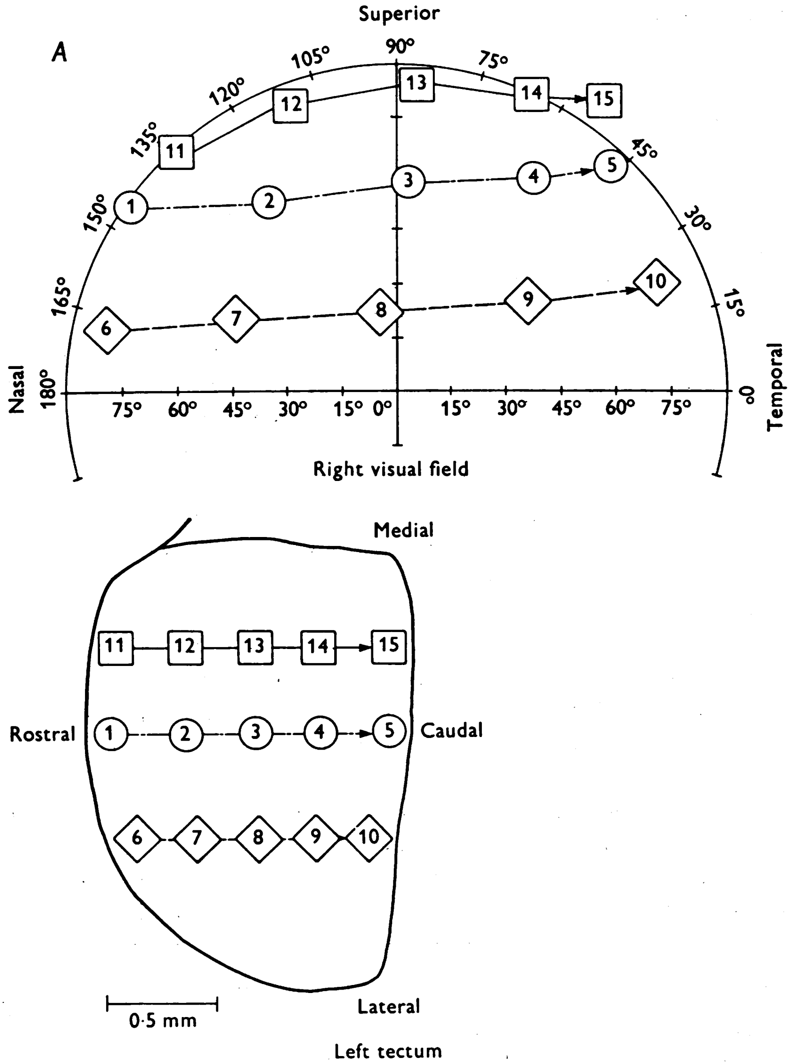
Four fish died prematurely. Retinotectal projections were tested for the other eight fish at post-operative intervals between 7 and 54 days. In three fish, tested, 7, 9, and 12 days after the surgery, neither the left half-tectum nor the right half-tectum gave any visual responses. The other five fish, tested 16, 18, 21, 24, and 28 days after the surgery showed that only the left rostral half-tectum became re-innervated at these stages. The newly restored retinotectal projections, however, did not show any sign of a field compression in all five fish. One of these maps is shown in Text-fig. 7. The map, obtained 28 days after the surgery, showed that only the nasal half of the right visual field projected on to the remaining rostral half of the left tectum. None of the rostral half of the right tectum in the five fish gave any visual responses at the same testing sessions. One of these fish was successfully revived after the first mapping experiment (18 days after the surgery). When the same fish was tested again 36 days later, it showed a field compression both in the left half-tectum and in the right half-tectum: the projections from the whole right visual field became compressed on to the remaining rostral half of the left tectum, and the whole left visual field also projected on to the remaining rostral half of the right tectum in correct retinotopic order.

The results show that optic fibres may re-innervate the rostral half of the left tectum as early as 16 days after section of the left optic tract near its entrance to the left tectum. At this early stage, however, the newly restored retinotectal projections retained a normal, uncompressed

---

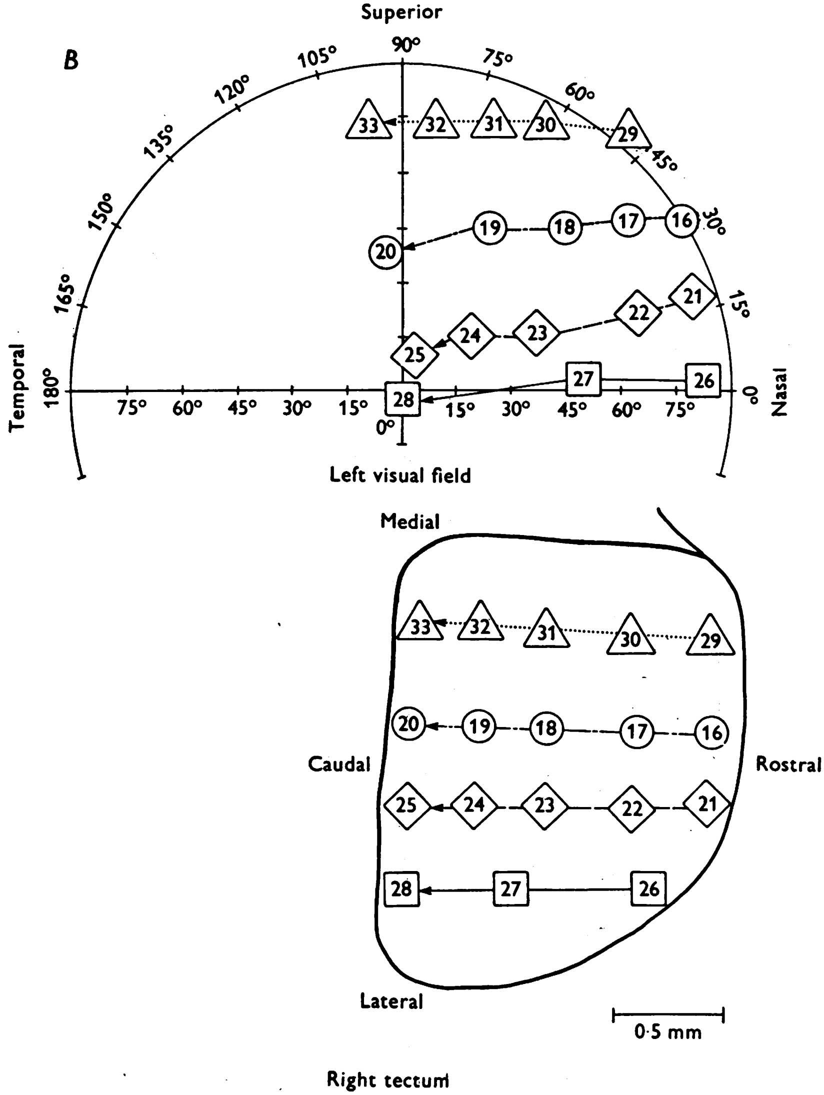
Text-fig. 7. Projection of the nasal half of the right visual field on to the rostral half of the left tectum in an adult goldfish. The retinotectal projection was mapped 28 days after excision of the caudal half of the left tectum and section of the left optic tract near its entrance to the remaining rostral tectum. The numbers marked on the enlarged drawing of the half-tectum indicate the loci of micro-electrodes on the dorsal view of the tectum in the order of recording visual responses from deep tectal layers. The corresponding numbers marked on the perimetric chart show the positions of the receptive fields in the contralateral visual field for the experimental points on the tectum.

In addition to the above surgery, the caudal half of the right tectum was also excised at the same time, and the left optic nerve was sectioned near the posterior pole of the left eyeball in the same fish (see Pl. 1). The remaining rostral half of the right tectum in this fish, however, did not give any visual responses at the same mapping session (28 days after the surgery).



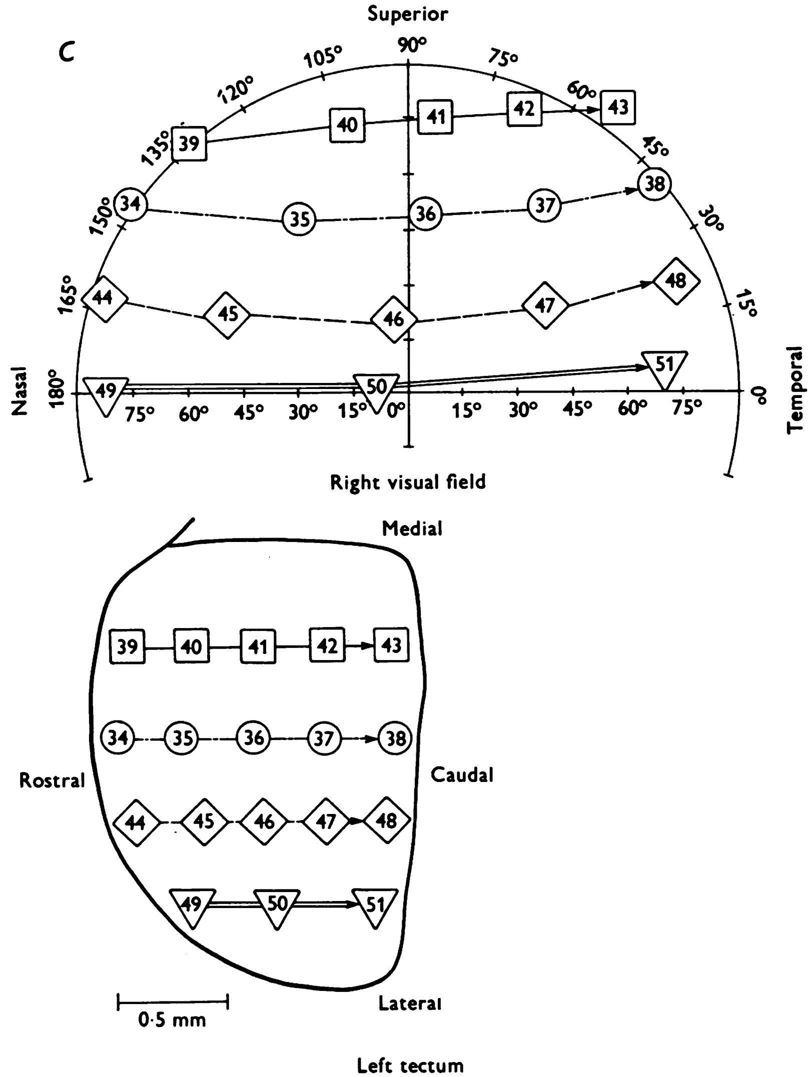
Text-fig. 8. Consecutive maps of retinotectal projections obtained at different post-operative periods following various surgical operations in an adult goldfish. *A*, was mapped 83 days after excision of the caudal half of the left tectum and section of the right optic nerve near the posterior pole of the right eyeball. The map shows that the re-established projections from the entire range of the right visual field is compressed on to the remaining rostral half of the left tectum in correct retinotopic order. Immediately after the first mapping session, the caudal half of the right tectum was excised, and both the left optic tract and the right optic tract were also sectioned near the entrances to their respective ipsilateral tecta in the same fish. *B*, shows the newly restored visual projection mapped

[*Continued on facing page*



Text-fig. 8*B*

19 days after excision of the caudal half of the right tectum and section of the right optic tract. The regenerated retinotectal projection retains a normal (uncompressed) pattern at this early stage. *C*, was obtained at the same mapping session as the map (*B*) from the same experimental fish. Note an orderly field compression in the map (*C*); the rostral half of the left tectum re-acquires projections from the whole right visual field within 19 days after section of the left optic tract (102 days after excision of the caudal half of the left tectum).



Text-fig. 8*C*. For legend see p. 636.

pattern (as late as 28 days after the surgery). The initially uncompressed state of the restored visual projections, however, eventually changed into a compressed pattern at a later stage (54 days after the surgery). What is responsible for this temporal transition? Does it reflect an ingrowing profile of regenerating optic fibres into the half-tectum? Or, is it due to a progressive topographic regulation of the halved tectum into a whole?

Experiment 4

In another group of twelve fish, the caudal half of the left tectum was excised. The remaining rostral half-tectum was also denervated by severing the right optic nerve near the posterior pole of the right eyeball at the same time. These fish were kept under a regular daily cycle of 12 hr in light and 12 hr in darkness.

One fish died during the recovery period. Retinotectal projections were mapped from the other eleven fish at post-operative intervals between 77 and 94 days. All eleven fish showed a field compression in their restored visual projections. One of these maps is shown in Text-fig. 8*A*. The map, obtained 83 days after the surgery, showed that the whole right visual field projected on to the remaining rostral half of the left tectum in an orderly compressed form. Immediately after the first mapping experiment, the caudal half of the right tectum was excised, and then both the left optic tract and the right optic tract were also sectioned near their entrances to the left half-tectum and to the right half-tectum, respectively, in each one of the eleven fish.

Six fish died during the recovery period after the second surgery. One fish, tested 20 days after the second surgery, did not give any visual responses from either tecta. The other four fish, however, yielded consistent results, one of which is shown in Text-fig. 8*B* and *C*. Both maps were obtained from the same fish at the same mapping session, 19 days after the second surgery. The newly re-established visual projections on to the rostral half of the right tectum (19 days after excision of its caudal part) retained a normal, uncompressed pattern: only the nasal half of the left visual field projected on to the recently halved right tectum as shown in Text-fig. 8*B*. On the other hand, the newly reconnected visual projections on to the rostral half of the left tectum (its caudal part was excised 102 days previously) in the same fish showed a complete field compression at the same testing session. Text-fig. 8*C* shows that the remaining rostral half of the left tectum reacquired visual projections from the entire right visual field in an orderly compressed pattern within 19 days after section of the left optic tract.

The same trend was also observed in the other three fish, tested 17, 20, and 22 days after excision of the caudal half of the right tectum, and section of both the right optic tract and the left optic tract (the caudal half of the left tectum in these fish was excised 106, 104, and 109 days, respectively, before the mapping experiments): the restored visual projection on to the more recently halved right tectum retained a normal, uncompressed pattern at this early stage, whereas the newly regenerated visual projection on to the left half-tectum in the same fish showed a field compression at the same testing session.

DISCUSSION

The present experiments on adult goldfish show that the pattern of a newly re-established visual projection on to a halved tectum depends on the duration of the post-operative period given to the halved tectum before it is re-innervated by incoming optic fibres from the retina. If the surgical operations are timed so that regenerating optic fibres invade the denervated rostral half-tectum earlier than a month following excision of the caudal tectum, the newly restored visual projection shows a normal, uncompressed pattern: only the nasal half of the visual field projects on to the remaining rostral half-tectum at this early stage. On the other hand, when a halved tectum received incoming optic fibres later than about 40 days following excision of the caudal tectum, a majority of the operated fish showed an initially compressed pattern in their newly reconnected visual projections. The results suggest that it takes at least a month of post-operative period for the halved tectum to be able to accommodate incoming optic fibres not only from the appropriate temporal area but also from the foreign nasal half of the retina in an orderly compressed topographic pattern.

A normal, uncompressed pattern of re-established visual projection on to a halved tectum (observed at an early post-operative period within 32 days after the tectal surgery) eventually changed into a compressed pattern as the post-operative period progressed. This temporal transition occurred in spite of a continual dark-deprivation of the operated fish. Under the present experimental conditions (which involved regeneration of optic fibres), the manipulation of post-operative visual environment turned out to be just a useless effort.

The temporal transition from a normal (uncompressed) pattern into an orderly compressed pattern of visual projection on to a halved tectum may well be due to intrinsic properties of the halved tectal tissue rather than due to those of regenerating optic fibres: the results of Experiment 4 (see Text-fig. 8) as well as those of Experiments 1 and 2 (see Text-fig. 4) show that the patterns of re-established retinotectal projection depend not on the time given to the regenerated optic fibres after their initial re-innervation of the halved tectum, but on the duration of post-operative periods given to the halved tectum following the tectal surgery. Thus, the temporal change in the topographic pattern may reflect the time course of progressive and systematic changes in the halved tectal tissue as a consequence of excision of the caudal half.

The present results are compatible with those of a previous work on adult goldfish (Yoon, 1972*a*): when a mechanical barrier was surgically inserted between the intactly innervated rostral half and the denervated caudal half of the tectum (the optic nerves were left intact), a sign of field compression gradually appeared first only in the medial side of the rostral half of the operated tectum at about 30 days after the surgery. The lateral side of the same half-tectum retained a normal projection at this early stage. About 1 or 2 months later, the field compression was found to have completed in the lateral side of the half-tectum as well. The gradual progress of the field compression was also observed by Cook & Horder (1974) after section of the optic nerve together with removal of the caudal half-tectum in goldfish. Their results are similar to those of the present Experiment 3 (in which the optic tract was sectioned) rather than those of the group $\Delta\tau = 0$, and the group $\Delta t = 0$ in Experiments 1 and 2 (in which the optic nerve was sectioned). Cook & Horder (1974) also reported that when the optic nerve was sectioned again, about 3 months after the previous surgery, the temporo-dorsal field was initially only partially represented (in the rostral half-tectum) but later a field compression recurred. The latter report does not agree with the present results (see Text-fig. 8 and also the scatter diagram in Text-fig. 4).

Recently, it has been found in adult goldfish that a piece of tectal tissue retains its original topographic polarity regardless of the orientation of re-implantation after either a rotation (Sharma & Gaze, 1971; Yoon, 1973, 1975*c*) or an inversion (Yoon, 1975*c*, *d*). The retention is not a transitory phenomenon. It persists as long as the re-implanted tectal tissue survives (Yoon, 1975*c*, *d*). The retention of the original topographic polarity by a piece of re-implanted adult tectal tissue suggests that the optic tectum is not a passive receiver of incoming optic fibres. Instead, the optic tectum should be regarded as an active accommodator, which selects appropriate optic fibres to make proper neural connexions according to the original polarities of the retinal tissue and of the tectal tissue in a consistent topographic order (Yoon, 1973, 1975*c*, *d*).

In this context of the optic tectum as an active accommodator, the dynamic re-organization of visual projections from the whole retina on to the rostral half-tectum suggests the following possibilities (Yoon, 1971, 1972*a*, *b*, 1973, 1975*a*, *c*, *d*); surgical excision of the caudal tectum may induce an activation of regulative mechanisms in the remaining rostral half-tectum. The half-tectum would undergo a topographic regulation from the halved gradient of its organizing factors into a whole, in reminiscence of an embryonic regulation (Spemann, 1938; Weiss, 1939). For example, the synaptogenic affinity factors of individual neurones, postulated by Sperry (1943*a*, *b*, 1944, 1945, 1951), may be re-specified by the regulative mechanisms according to the new relative positions of the visual neurones within the half-tectum. Thus, the halved tectal tissue eventually acquires a complete rostrocaudal gradient of the tectal affinity factors. This topographic regulation would enable the halved tectum to accommodate incoming optic fibres not only from the temporal hemiretina but also from the nasal hemiretina in an orderly compressed topographic pattern.

The results of the present time series experiments are compatible with the above interpretation: the post-operative period of at least a month (which was required to induce a field compression in the halved tectum) is not unrealistically short for the postulated regulative processes of neuronal re-specification to occur in the halved tectal tissue. At the present, nothing is known about the nature of the biological factors which are involved in the original specification of the tectal neurones, let alone the further complexities involved in their re-specification. Then, why is the possibility of the neuronal re-specification discussed here? The time course of re-specification (as inferred indirectly from the present experiments) provides us with one of the criteria to be used for biological identification of the hypothetical factors responsible for neuronal specification.

I wish to thank F. Baker for his technical assistance. The research was supported by grants from the Medical Research Council (MT 4994) and from the National Research Council (A 9756) of Canada, while the author held a Killam research professorship.

REFERENCES

COOK, J. E. & HORDER, T. J. (1974). Interactions between optic fibres in their regeneration to specific sites in the goldfish tectum. *J. Physiol.* **241**, 89–90*P*.

CROSSLAND, W. J., COWAN, W. M., ROGERS, L. A. & KELLY, J. P. (1974). The specification of the retinotectal projection in the chick. *J. comp. Neurol.* **155**, 127–164.

GAZE, R. M. (1970). *The Formation of Nerve Connections*. New York: Academic Press.

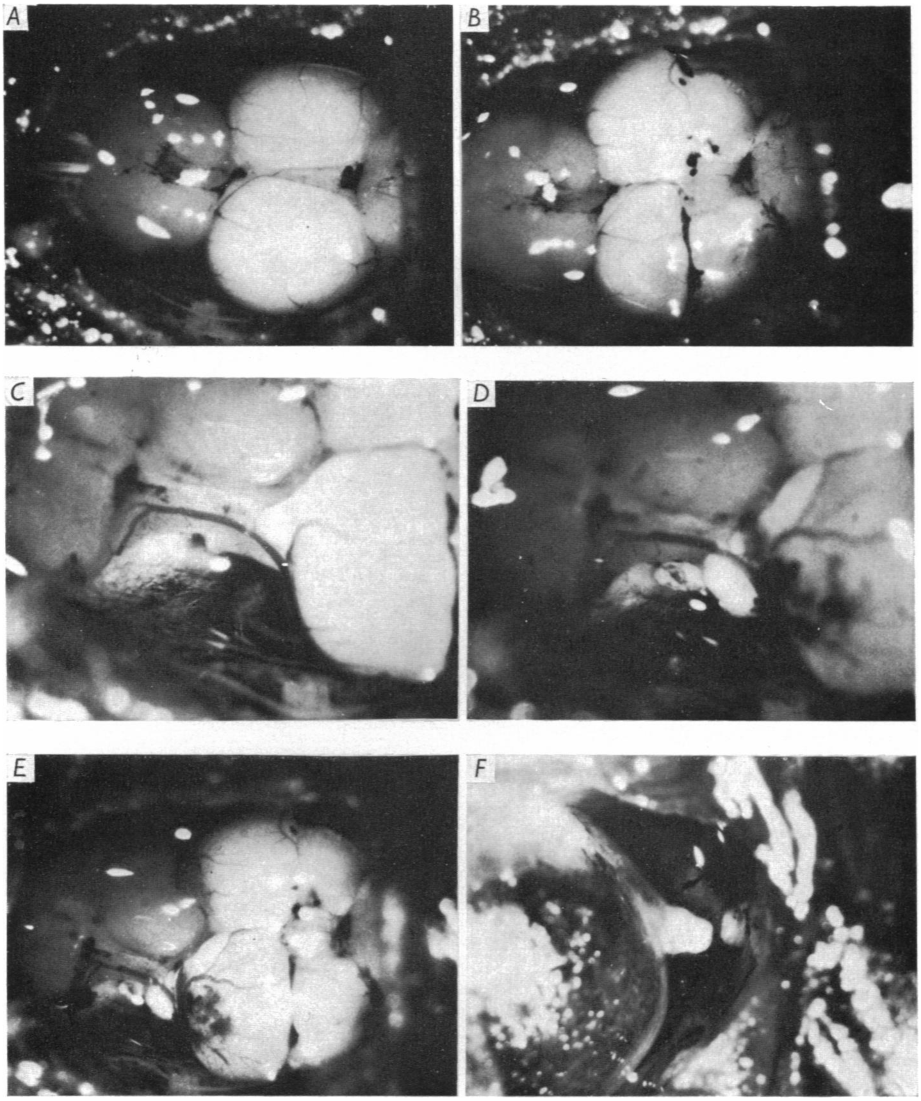
GAZE, R. M. & SHARMA, S. C. (1970). Axial differences in the reinnervation of the goldfish optic tectum by regenerating optic fibers. *Expl Brain Res.* **10**, 171–181.

HUNT, R. K. & JACOBSON, M. (1974). Neuronal specificity revisited. *Curr. Tops Devl Biol.* **8**, 203–259.

JACOBSON, M. (1970). *Developmental Neurobiology*. New York: Holt, Rinehart and Winston.

MEYER, R. L. & SPERRY, R. W. (1974). Explanatory models for neuroplasticity in retinotectal connections. In *Plasticity and Recovery of Function in the Central Nervous System*, ed. STEIN, G., ROSEN, J. J. & BULLERS, N., pp. 45–63. New York: Academic Press.

SHARMA, S. C. (1972*a*). Reformation of retinotectal projections after various tectal ablations in adult goldfish. *Expl Neurol.* **34**, 171–182.



MYONG G. YOON

(*Facing p.* **643**)

Sharma, S. C. (1972*b*). Redistribution of visual projections in altered optic tecta of adult goldfish. *Proc. natn. Acad. Sci. U.S.A.* **69**, 2637–2639.

Sharma, S. C. & Gaze, R. M. (1971). The retinoptic organization of visual responses from tectal reimplants in adult goldfish. *Archs ital. Biol.* **190**, 357–366.

Spemann, H. (1938). *Embryonic Development and Induction.* New Haven, Conn: Yale University Press.

Sperry, R. W. (1943*a*). Visuomotor coordination in the newt (*Triturus viridescens*) after regeneration of the optic nerves. *J. comp. Neurol.* **79**, 33–55.

Sperry, R. W. (1943*b*). Effect of 180 degree rotation of the retinal field on visuomotor coordination. *J. exp. Zool.* **92**, 263–279.

Sperry, R. W. (1944). Optic nerve regeneration with return of vision in *Anurans*. *J. Neurophysiol.* **7**, 57–70.

Sperry, R. W. (1945). Restoration of vision after crossing of optic nerves and after contralateral transplantation of eye. *J. Neurophysiol.* **8**, 15–28.

Sperry, R. W. (1951). Regulative factors in the orderly growth of neural circuits. *Growth Symp.* **10**, 63–87.

Sperry, R. W. (1965). Embryogenesis of behavioural nerve nets. In *Organogenesis*, ed. De Hann, R. L. & Ursprung, H., pp. 161–186. New York: Holt, Rinehart and Winston.

Weiss, P. (1939). *Principles of Development.* New York: Holt, Rinehart and Winston.

Yoon, M. G. (1971). Reorganization of retinotectal projection following surgical operations on the optic tectum in goldfish. *Expl Neurol.* **33**, 395–411.

Yoon, M. G. (1972*a*). Reversibility of the reorganization of retinotectal projection in goldfish. *Expl Neurol* **35**, 565–577.

Yoon, M. G. (1972*b*). Transposition of the visual projection from the nasal hemiretina onto the foreign rostral zone of the optic tectum in goldfish. *Expl Neurol.* **37**, 451–462.

Yoon, M. G. (1973). Retention of the original topographic polarity by the 180 degree rotated reimplant in young adult goldfish. *J. Physiol.* **233**, 575–588.

Yoon, M. G. (1975*a*). Effects of post-operative visual environments on reorganization of retinotectal projection in goldfish. *J. Physiol.* **246**, 673–694.

Yoon, M. G. (1975*b*). Time-course of the topographic regulation of a halved optic tectum in adult goldfish. *Neurosci. Astr.* **1**, 115.

Yoon, M. G. (1975*c*). Topographic polarity of the optic tectum studied by reimplantation of the tectal tissue in adult goldfish. *The Synapse, 40th Cold Spring Harb. Symp. Quant. Biol.* (in the Press).

Yoon, M. G. (1975*d*). Re-adjustment of retinotectal projection following reimplantation of a rotated or inverted tectal tissue in adult goldfish. *J. Physiol.* **252**, 137–158.

EXPLANATION OF PLATE

Microphotographs of the dorsal view of the visual pathways in an experimental goldfish. *A*, shows the two intact optic tecta in the mid-brain. *B*, shows the remaining rostral halves of the tecta after surgical excision of their caudal parts. *C*, shows the intact left optic tract, emerging from the optic chiasm beneath the forebrain. The posterior part of the left forebrain was removed in order to expose the left optic tract. *D*, shows the left optic tract, severed just before it bifurcates into the medial branch and the lateral branch. *E*, shows the over-all view of the operated visual pathways in the mid-brain. *F*, shows the left optic nerve sectioned near the posterior pole of the left eyeball.