RETINAL PROJECTIONS IN THE AUSTRALIAN LUNGFISH

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SUMMARY

Autoradiographic analysis of the primary retinofugal projections in the Australian lungfish reveals contralateral retinal projections to a ventral portion of the periventricular preoptic nucleus, throughout its rostrocaudal extent, and to 4 distinct terminal fields in the thalamus. Only one of these thalamic fields (t4) likely receives dendrites solely from dorsal thalamic neurons. Thalamic terminal field 1 probably receives dendrites from both dorsal and ventral thalamic neurons, and fields 2 and 3 from only ventral thalamic neurons. Contralateral retinofugal fibers terminate in the pretectum and in the superficial and central tectal zones. The central tectal terminal field is restricted to the medial one-third of the tectum. At pretectal levels a contralateral basal optic tract arises from the marginal optic tract and terminates along the lateral edge of the tegmentum, as a series of glomerular puffs, and in the rostral pole of a superficial isthmal nucleus. The Australian lungfish, unlike the African and South American lungfish, possesses ipsilateral retinal projections to all of the nuclei that receive contralateral retinal input.

INTRODUCTION

The living lungfish or dipnoans represent the remnants of a once flourishing radiation of bony fishes whose members exhibit several similarities to crossopterygians — the osteichthian radiation that gave rise to land vertebrates. The exact phyletic relationship of the dipnoans to other fishes is uncertain, and two interpretations of their anatomy have been offered. Romer[6] argued that the lungfishes are more closely related to the crossopterygians than to the ray-finned fishes; whereas Schaeffer[7] argued that the dipnoans are a separate radiation of bony fishes, equally distinct from lobe-finned and ray-finned fishes.

Regardless of which hypothesis is correct, the brain of dipnoans is far more similar to that of the living crossopterygian, *Latimeria chalumnae*, than to ray-finned
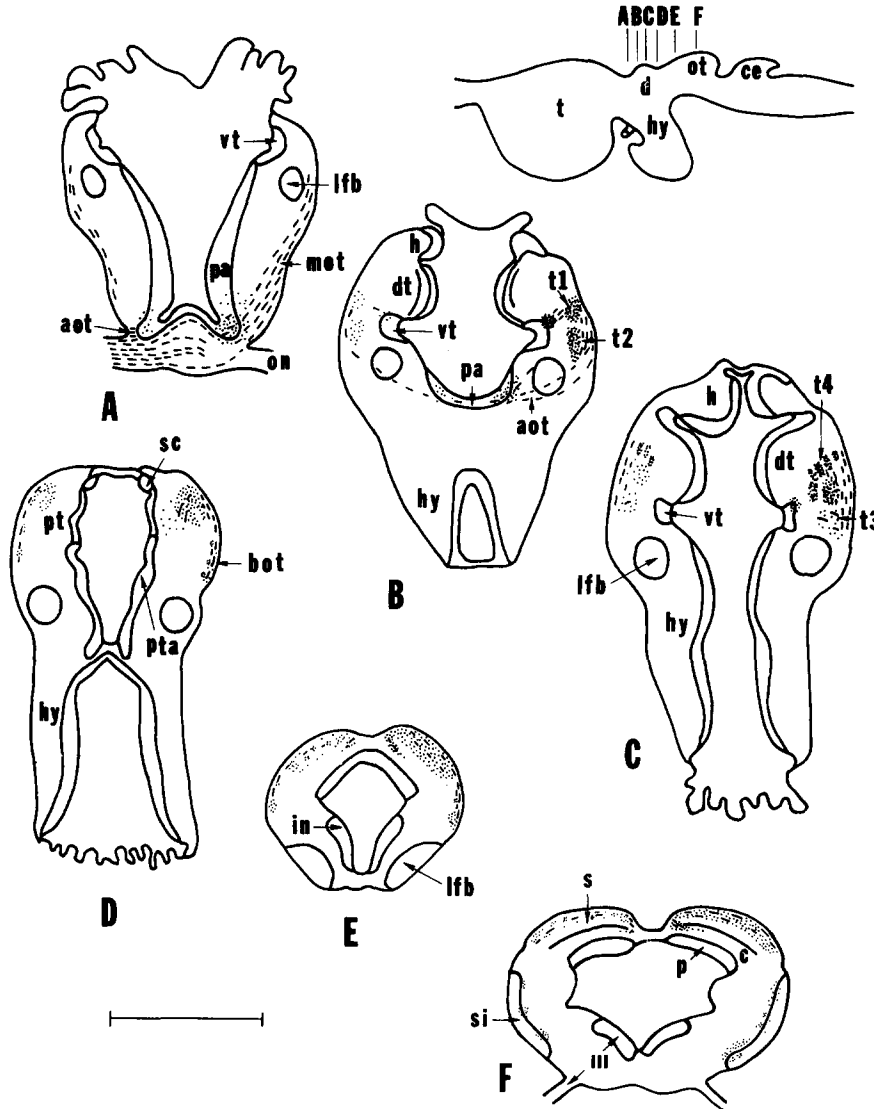
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Fig. 1. Charting of the primary retinofugal projections following intraocular injection of [³H]proline. A–F: transverse sections through the diencephalon and mesencephalon at levels indicated on the lateral view of the brain. Fine stippling indicates terminal fields, and dashed lines fibers of passage. Contralateral retinal projections are charted to the right and ipsilateral projections to the left. Bar scale equals 2 mm. Abbreviations: aot, axial optic tract; bot, basal optic tract; c, central tectal zone; ce, cerebellum; d, diencephalon; dt, dorsal thalamus; h, habenula; hy, hypothalamus; in, interstitial nucleus; lfb, lateral forebrain bundle; mot, marginal optic tract; on, optic nerve; ot, optic tectum; p, periventricular tectal zone; pa, preoptic area; pt, pretectum; pta, posterior tuberal area; s, superficial tectal zone; sc, subcommissural organ; si, superficial isthmal nucleus; t, telencephalon; t1–t4, thalamic retinal terminal fields; vt, ventral thalamus; III, oculomotor nucleus and nerve.

fish. Latimeria is an extremely rare species. Some 70 specimens have been captured, but none have survived more than a few hours. Thus, it is unlikely that experimental details of its neuroanatomy will be available in the near future. However, experimental neuroanatomical study of the living lungfish is possible and will greatly increase our knowledge of the CNS of lobe-finned fish, much of which is likely applicable to Latimeria. In this regard, the Australian lungfish, *Neoceratodus fosteri*, is particularly interesting as this species is considered the most primitive living lungfish[3] and, of all the lungfish, its brain is most similar to that of Latimeria[5]. Unfortunately, the Australian lungfish is a rare and endangered species, and there are few opportunities to study it. However, a single individual recently became available to me, thus affording me the opportunity to experimentally examine its retinal projections and to complete a survey of these pathways in all dipnoan genera[4].

MATERIALS AND METHODS

A single specimen of Neoceratodus (a 6.1 kg adult) received an intraocular injection of 100 μCi of [^{3}H]proline under MS222 anesthesia and was allowed to survive 4.5 days at 23–25 °C. The animal was perfused with a mixture of 1% gluteraldehyde–2.5% paraformaldehyde, and the brain was subsequently embedded in paraffin. Fifteen-μm sections of the brain were cut in the transverse plane; the sections were coated with Kodak NTB3 emulsion and exposed for 30 days. The exposed sections were developed in Kodak Dektol and stained with cresyl violet. The retinofugal projections are charted in Fig. 1, and the nomenclature employed is essentially that of Holmgren and van der Horst[2].

RESULTS

Optic nerve fibers turn medially in the optic chiasm where the majority, but not all, decussate to form the marginal optic tract (Fig. 1A). At the level of the decussation, some fibers turn dorsomedially and terminate in the ventral part of the periventricular preoptic nucleus (Fig. 1A). This retinal terminal field extends to the caudal pole of the preoptic nucleus (Fig. 1B). As the marginal optic tract courses dorsally and caudally in the rostral thalamus, two distinct retinal terminal fields are recognized (Fig. 1B).

The dorsal field (t1) is the most dense, and small tongue-like fiber bridges course medially to terminate in the periventricular cell plate of the ventral thalamus. This first terminal field and its medial extension occupy the rostral half of the thalamus.

More ventrally, a second terminal field (t2, Fig. 1B) occurs medial to the optic tract and constitutes the most dense ventral thalamic retinal field. More caudally, a third terminal field (t3, Fig. 1C) arises ventral to the second terminal field and can be traced to the end of the ventral thalamus.

A fourth terminal field arises at mid-thalamic levels (t4, Fig. 1C) and is the only one of the 4 fields that likely receives only dendrites of the dorsal thalamus. This fourth field occupies the lateral half of the thalamic wall and primarily consists of a dense
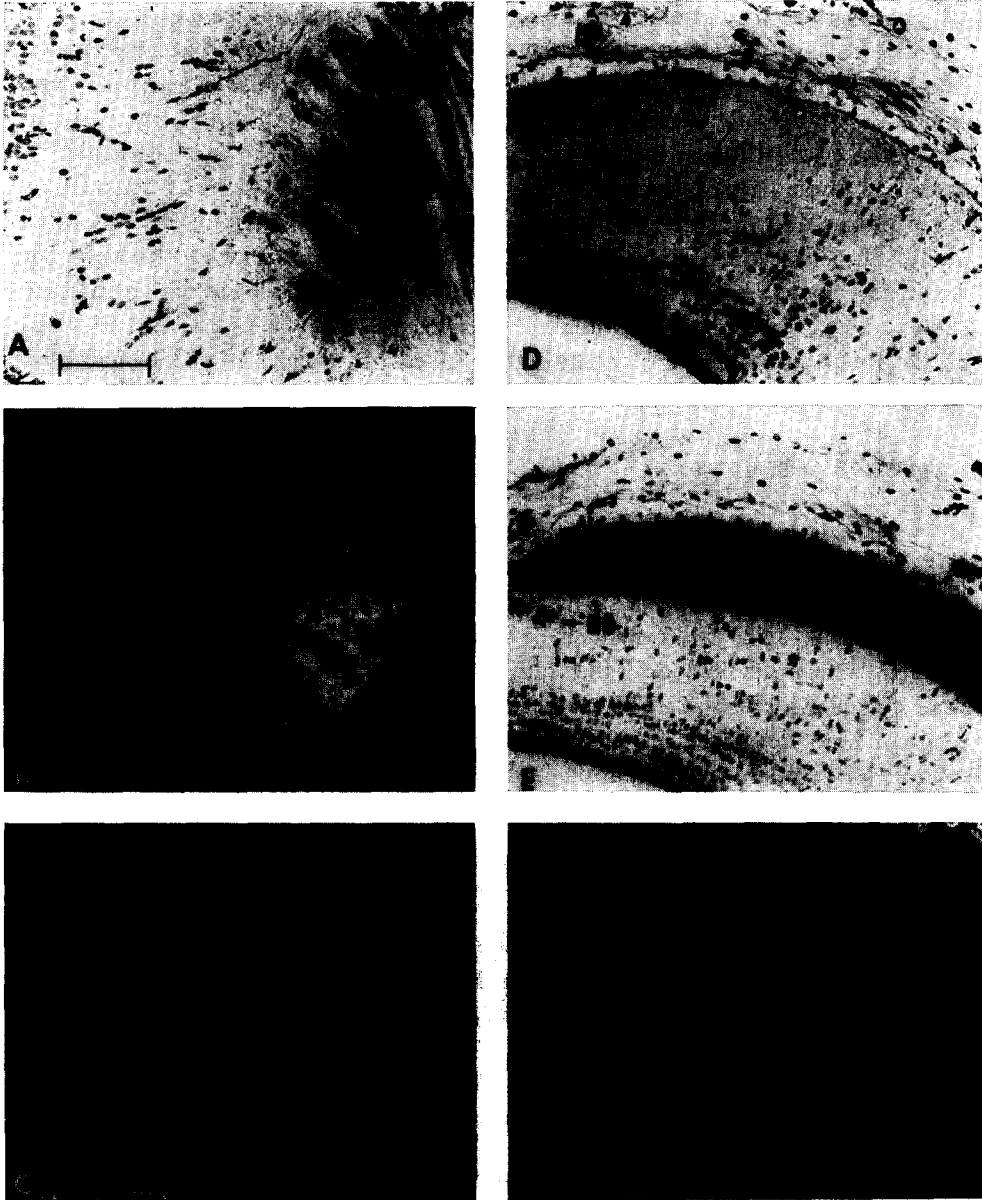
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Fig. 2. Photomicrographs of Neoceratodus diencephalon and mesencephalon. A: transverse section through the right dorsal thalamus illustrating optic tract bundles and terminal neuropil (darker fibers) as well as non-retinal fibers (large light bundles to right of photograph). B: transverse section through comparable dorsal thalamic area illustrating labeled optic tract fibers and terminals of contralateral projection. C: labeled optic tract fibers and terminals of ipsilateral projection to dorsal thalamus. D: right optic tectum illustrating migrated neurons and boundaries of periventricular (p), central (c) and superficial (s) tectal zones. E: contralateral retinal projections to outer half of superficial tectal zone, and medial deep optic fascicle (do) which projects to boundary area of superficial and central tectal zones. F: ipsilateral retinal projection to left optic tectum. Terminals appear to end as distinct grain puffs. Magnification of A, B, D and E is identical and bar scale equals 200 μm. Magnification of C and F is identical and bar scale equals 7 μm.

neuropil (Fig. 2A). A few thalamic cells are located adjacent to the neuropil, but the bulk of the thalamic cells form a laminated periventricular plate. The thalamic neuropil consists of optic fibers and terminal patches intersected by fascicles of non-retinal fibers, giving the fourth terminal field a laminated appearance (Figs. 1C, 2A and B). This terminal field continues to the caudal pole of the dorsal thalamus and is the single largest thalamic retinal target.

A distinct bundle of optic fibers, the axial optic tract (aot, Fig. 1A and B), occupies the most caudal portion of the chiasm; these fibers are the last optic fibers to decussate. They form a distinct bundle rostrally, but eventually join the marginal optic tract.

As the marginal optic tract continues caudally, it gives rise to a dense, outer pretectal terminal field and a more sparse, inner pretectal terminal field (Fig. 1D). The outer field is C-shaped with a ventrolaterally directed notch marking the position of the fasciculus retroflexus. The pretectum consists primarily of a lateral neuropil and a periventricular cell plate, although a few neurons do constitute a rudimentary central migrated nucleus. Thus, the pretectum of Neoceratodus consists of central and periventricular pretectal nuclei.

A distinct basal optic tract arises at pretectal levels (Fig. 1D) and courses ventrally and caudally. Throughout its caudal course, small puffs of dense label are seen scattered among the more sparse, linearly arrayed grains, suggesting that the basal optic tract terminates in a series of scattered glomerular-like terminal fields. Optic fibers are continually added to the basal optic tract from pretectal to rostral tectal levels (Fig. 1E); more caudally the basal optic tract appears as a separate slip that terminates in the superficial isthmal nucleus (Fig. 1F). This nucleus is a distinct population of granular-like cells forming a continuous sheet over the lateral tegmental wall; it is seen in all lungfish and in *Latimeria chalumnae*.

The optic tectum of Neoceratodus is more differentiated than that of the other dipnoans, and Neoceratodus is the only species that possesses migrated neurons forming distinct central and superficial tectal zones (Fig. 2D). As the marginal optic tract approaches the rostral pole of the optic tectum, it forms medial and lateral subdivisions which course through the upper half of the superficial tectal zone (Figs. 1E, F and 2E). The retinal recipient tectal zone consists of 3 alternating layers of optic fibers and their deeper terminal fields.

One additional optic fascicle arises from the ventral edge of the medial optic tract (Figs. 1E, F and 2E) and courses laterally, terminating at the boundary of the superficial and central tectal zones. A comparable fascicle does not appear to arise from the lateral optic tract.

DISCUSSION

Unlike the other dipnoans[4], Neoceratodus possesses ipsilateral retinal pathways. A small, but distinct, portion of the optic fibers do not decussate, but turn caudally to form uncrossed components in the axial, basal and marginal optic tracts (Fig. 1A–F). The ipsilateral retinal fibers appear to terminate in all diencephalic and mesencephalic

nuclei that receive contralateral retinal efferents. The ipsilateral retinal projection to the dorsal thalamus (t4) appears to be restricted primarily to the outer half of the neuropil (Fig. 2C) and may not overlap the portions of the neuropil that receive contralateral input. However, additional specimens are needed to accurately assess this segregation.

The ipsilateral projection to the optic tectum does not form a dense continuous sheet but consists of distinct puffs (Fig. 2F) like those characterizing ipsilateral retinotectal projections in mammals[1]. Unlike mammals, the ipsilateral retinotectal projection in Neoceratodus extends throughout the entire rostrocaudal tectal axis.

The retinal projections in Neoceratodus are similar to those of the other dipnoans[4] in that essentially the same number of retinal targets are seen in both dipnoan families. However, only Neoceratodus possesses ipsilateral retinal efferents. The eyes of Neoceratodus are larger and better developed than those of other lungfish, and these differences are clearly reflected in its CNS by the relatively large, differentiated dorsal thalamus and pretectum and by a laminated optic tectum. Finally, a distinct retinal fascicle to the central tectal zone characterizes Neoceratodus but is not seen in the other lungfish.

This study completes a retinal survey of dipnoans and the data, compared to extensive information in the literature on amphibian visual projections, should allow a meaningful analysis of the visual organization of Latimeria.

ACKNOWLEDGEMENTS

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