Independent Biaxial Reorganization of the Retinotectal Projection: A Reassessment

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Summary. It has been previously suggested that the retinotectal projection can reorganize independently along two orthogonal tectal axes. This possibility was reexamined by removing roughly a quarter of the retina and slightly less than a quarter of the tectum. In the tectal case, the unseated fibers arborized rostral to the ablation, but not lateral to it, and the projection shifted irrespective of tectal axes to maintain topographic order and a roughly uniform representation of retinal areas. In the retinal case, expansion into the denervated quadrant was only from the rostral, never from the medial or lateral directions. Analysis of the movements of fiber arbors shows that they respond to local competition for tectal space rather than following tectal axes.

Key words: Goldfish – Retinotectal reorganization – Competitive innervation

The early experiments of Attardi and Sperry (1963) and Jacobson and Gaze (1965) appeared to establish the immutability of the retinotectal projection in goldfish. In the first of these, portions of the retina were removed and the optic nerve crushed, and the regenerating fibers arborized only at the sites previously occupied, often bypassing other sites vacated as a result of the retinal lesion. In the second report, the medial or lateral half of one tectal lobe was removed and the nerve crushed, and the subsequent retinotectal projection originated only from the part of the retina which had previously projected to the remaining hemi-tectum. Neither case demonstrated any capacity for modifying the retinotectal map.

Later Gaze and Sharma (1970) reported that, within months after the caudal half tectum was removed, the entire retinal projection became compressed onto the remaining hemi-tectum. They concluded from this and the earlier study

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(Jacobson and Gaze, 1965) that the two tectal axes differed; compression was possible rostrocaudally but not mediolaterally.

This compromise was rejected by Yoon (1971) who suggested that the failure to demonstrate mediolateral compression stemmed from the surgery. Ordinarily, the retinal fibers which terminate in the dorsal tectum enter rostrally and course, like the rays of a fan, toward their terminations (Leghissa, 1955). Yoon contended that the medial and lateral lesions, which extended to the rostral pole of the tectum, might have prevented many fibers from entering. Accordingly, he spared the rostral pole and removed less than a quarter of the tectum, in the caudomedial quadrant. Following this procedure, the retinotectal projection reorganized so that the dorsalmost portion of the visual field shifted laterally, from its normal position at the medial boundary of the tectum, to the medial edge of the lesion. Likewise, some areas of the visual field sometimes projected nearer the rostral pole than before. These shifts were interpreted as independent and simultaneous compression along the two tectal axes.

The notion of two independent orthogonal axes across both the retina and the tectum is rooted in Sperry's (1943, 1963) theory of neuronal specificity. Experimentally, two such retinal axes appear to be independently established at different developmental stages, both in salamanders (Székely, 1954) and frogs (Jacobson, 1968). Corresponding tectal axes have never been demonstrated (Chung and Cooke, 1975), but are assumed to direct innervation through the matching of each tectal position, determined with respect to the two tectal axes, with fibers from the corresponding retinal position, determined with respect to its two axes. Gaze and Sharma (1970) suggested that compression becomes possible if it is the relative (rather than absolute) position along the remaining tectal axis that is relevant in the matching process. If so, one might expect independent compression along the two tectal axes following quarter tectal ablation, as Yoon (1971) appears to find. However, the evidence presented was weak, since if biaxial compression did occur, two strong predictions can be made, neither of which was tested. First, the points in the visual field which previously projected to the missing tectal quadrant should, following compressive reorganization, project to two widely separate tectal areas (Fig. 1B). This seems intuitively unlikely since it requires that many of the fibers severed at the rostral boundary of the lesion must grow laterally, turn the corner around the lesion, and then run caudally, in order to terminate at a new site in the caudolateral quadrant. The second prediction concerns the magnification factor (the number of μm on the tectum per degree in the visual field). The rostrocaudal and mediolateral magnification factors (RCMF and MLMF respectively) should differ markedly in the three remaining quadrants (Fig. 1C). Specifically, the RCMF should be reduced only in the rostromedial quadrant, and the MLMF only in the caudolateral quadrant; both should remain normal elsewhere. Yoon (1971) noted decreases in the predicted regions, but there were too few points (typically 15 to 20 in the whole map) to assess it elsewhere. Double representation of some points in the visual field was suggested in one of his two maps (Fig. 7), but the issue was not treated directly.

We have reexamined the question by making similar lesions and analyzing the subsequent projections with particular attention to the predictions above.