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Two distributions of axons in the optic nerve of quails: a study of nerve degeneration after laser lesions of the retina

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Order in the optic pathway has been under close scrutiny since the last century. In fishes, the position of the axons along the optic nerve is a function of the position or of the age of the corresponding neuronal body in the retina[5,12,13]. However, in cats, optic axons only show a crude retinotopic order[8]. Our observations in the quail showed the existence of at least two kinds of axons according to their position in the optic nerve. Although some axons were found in close spatial relationship with others originating in the same region of the retina, other axons occupied positions independent of their site of origin in the retina.

The right eyes of male quails (*Coturnix coturnix*) were irradiated with an argon laser operated at 514.5 nm[4]. In another group of birds, the right retina was surgically destroyed. Quails were decapitated after one week. Right and left optic nerves were fixed in glutaraldehyde and post-fixed in osmium tetroxide. Semi-thin sections (1.5–4.0 μm) were stained with *p*-phenylenediamine[7].

Both laser irradiation and surgical destruction of the retina produced the same type of structural alterations in the optic nerve. The amount of degenerating axons depended on the size of the lesion. These axons appeared either as dark fibers or as swollen fibers with a clear axoplasm. Only the former were scored. The irradiated region contained both ganglion cell somata and axons coming from the periphery[3]. Thus, the damaged axons belonged to a retinal territory of sectorial shape with its apex pointing to the nerve-head and its base close to the edge of the retina.

Seven birds were irradiated with 1.8 W for 15 s. Axons were destroyed from a 60–90° sector with its apex close to the nerve-head. The nerve cross-sections of some birds showed a dark stripe containing all the degenerating axons. In other birds, the degenerating fibers spread over most of the nerve cross-section. The striped pattern corresponded to lesions of the ventral retina, whereas the diffuse pattern correlated with lesions in the dorsal retina.

Smaller lesions were made with 0.5 W for 1 s (Fig. 1). These retinas were flat-mounted[3] and the size and position of the lesions were ascertained with an ocular micrometer. The position of the lesions was referred to a pair of cartesian coordinates where the y axis coincided with the nerve-head and the x axis

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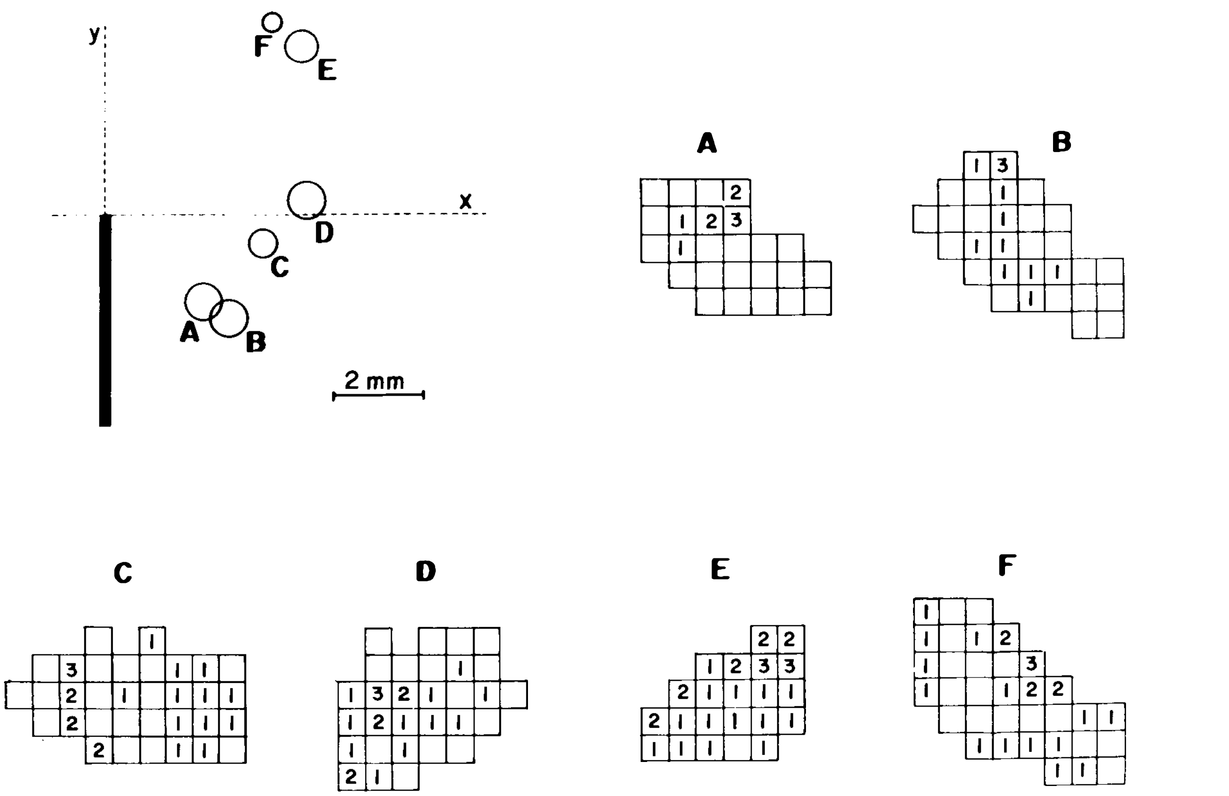

Fig. 1. Distribution of degenerating fibers after small lesions. Their localization on the anterior hemiretina is shown in the upper left corner. Axis y corresponds to the pecten. This is depicted as a thick black line. A–F: sections from the corresponding optic nerves. Dark axons were scored on each square (17,000 μm^2). In each section, a 100% value was assigned to the square with the highest density. Squares with 10% or less of the maximum value were considered non-significant. 1, 11–40%; 2, 41–70%; 3, 71–100%.

crossed it through its most dorsal point. These lesions were practiced on the anterior (or nasal) hemiretina, at a certain distance from the nerve-head. Their diameter was 0.8 mm or less. Although the amount of degenerating axons was much lower than before, the same two patterns were observed. These experiments showed that the axons of ganglion cells ventral to the x axis, traveled together. Axons originating dorsally to the x axis traveled without any apparent order. Birds with a lesion very close to the x axis yielded a mixed distribution where both a striped and a diffuse pattern could be discerned. These patterns were maintained throughout the entire nerve and chiasma.

Since we have never found any resemblance between the shape of the retinal lesion and the distribution of degenerating axons in the nerve, we must conclude that optic fibers do not keep the same neighbors along their route to the brain. However, the striped pattern might be considered to be a transformation of the distribution of ganglion cell somata. According to the models presented for fishes[1,12] the nerve-head (or choroid fissure) is represented on the surface of the nerve. Results obtained with the smaller lesions suggest that this would not be the case for quails. Larger lesions affected the most central ganglion cells. Although the smaller lesions spared these neurons, the resulting stripes were equal in length, but thinner than those derived from the larger lesions. Since it has been shown in the chick[11] that axons from the central retina occupy central positions in the nerve, it can be postulated that stripes contain all the axons entering the nerve through a certain point of the nerve-head.

The existence of two groups of fibers is not a peculiarity of quails. Axons traveling with different degrees of retinotopical organization have been described in *Amblystoma*[6] and primates[9,10]. Besides, fibers in the nervous system do not necessarily sort themselves out according to their topographical origin, but can also do so according to their modality (refs. 2, 14).

It must be emphasized that the absence of a retinotopic organization in the nerve of adult birds does not imply its absence during the first stages of embryogenesis. On the other hand, the coexistence of two patterns of axonal distribution suggests that events occurring at the level of the choroid fissure (or its successor: the nerve-head) would not be the only factors determining the final organization of the visual pathways.

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