DEVELOPMENT AND PLASTICITY OF THE TECTOFUGAL VISUAL PATHWAY IN THE ZEBRA FINCH

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INTRODUCTION

In the recent years the development of the visual system of mammals and its alterability by environmental influences has been addressed by hundreds of investigations. Detailed knowledge on the development and plasticity of the visual cortex, for example, has been accumulated for a variety of mammals, in particular cats and monkeys (rev. Fregnac and Imbert 1984). In contrast, very few studies were concerned with the development of higher stations of the visual system of other vertebrates. In birds, for example, the retinotectal projection of the chick tectofugal pathway is one of the best investigated paradigms for the development of the specificity of neuronal connections and axonal pathfinding (see Thanos, this volume); however, there were almost no developmental studies of other stations of the tectofugal pathway until recently. In one of the earliest studies Pettigrew and Konishi (1976a,b) showed that the visual wulst has physiological properties very similar to those of the visual cortex in mammals, and that monocular deprivation in these animals induces the same shift in ocular dominance of wulst neurons as it was observed in area 17 of the cat or the monkey.

Owls, however, are not necessarily a representative example of the avian phylum because their eyes are located frontally. Most other species of birds have rather laterally placed eyes. We therefore investigated the development and plasticity of the visual pathway of the zebra finch, a small altricial bird which has recently become a standard laboratory animal because it is easy to keep and has a short reproduction cycle of about 70 days.

Eyes of zebra finches are situated laterally in the head and the optical axes of the eyes are diverging by about 120 degrees (Bischof 1988). As in most birds, the tectofugal pathway, which is equivalent to the visual pathway, leading to the extrastriate cortex in mammals, is much more developed than the thalamofugal projection in the zebra finch. In pigeons, another laterally-eyed bird, the tectofugal pathway plays a prominent role in tasks which are to be said to be a property of the thalamofugal pathway in mammals, as for example the discrimination of patterns or color (Hodos and Karten 1966, Hodos 1969).

Instead of giving a complete overview of our experiments, we intend here to describe the main features of the development of the tectofugal pathway in the zebra finch. Moreover, we want to give some information about the effects of monocular deprivation on the development of this projection, and the existence of a sensitive period during which these effects are most prominent.

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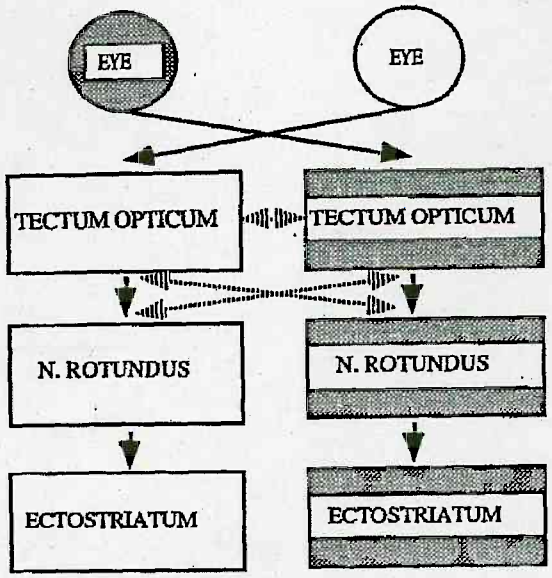

Fig. 1. Simplified diagram of the tectofugal pathway in birds. The cap over one eye symbolizes deprivation. Stippled areas: areas referred to in the text as "deprived eye" or "deprived hemisphere", respectively. Stippled lines: Interhemispheric connections.

VISUAL PATHWAYS IN BIRDS

The avian visual system differs from the mammalian in several aspects. The most important difference is that the avian optic nerve is crossing almost completely to the contralateral hemisphere. From the optic chiasm, two main projections can be traced in birds. The thalamofugal pathway leads from the eye to a variety of thalamic nuclei, commonly called the OPT (opticus principalis thalami) complex and then to a telencephalic target area called visual wulst. This pathway is comparable to the geniculocortical pathway in mammals (Karten 1979, Karten and Shimizu 1989), because the visual wulst has many similarities with the area 17 of the visual cortex in mammals, as was demonstrated by electrophysiological (Pettigrew and Konishi 1976a,b) histochemical (Shimizu and Karten 1990), and tracing studies (Bagnoli et al. 1982).

The second projection, the tectofugal pathway, is the most prominent in most avian species. Retinal ganglion cell fibers project to the mesencephalic optic tectum, the visual information is then transferred to the nucleus rotundus of the thalamus and further to the telencephalic ectostriatum (fig.1). Based on anatomical and physiological data, this pathway has been compared to the mammalian projection to the extrastriate cortex (Karten and Shimizu 1989). Most probably, the ectostriatum is comparable to layer 4 of the extrastriate cortex, whereas the other neocortical layers are represented in birds by other structures of the dorsal ventricular ridge, namely the neostriatum and the archistriatum (Karten and Shimizu 1989).

Due to the almost total crossing of the optic nerve, the visual information of each eye is primarily restricted to the contralateral hemisphere. Interaction of the two hemispheres, however, can be accomplished by a variety of recrossing projections, which have been demonstrated for both the thalamofugal and the tectofugal pathway. Based on experiments in the owl (Bravo and Pettigrew 1981), the thalamofugal pathway has been seen as to processing mainly binocular information from the frontal visual field, whereas the tectofugal pathway has been said to receive input from the lateral visual field. Binocular processing within the tectofugal pathway was considered to be negligible, because the recrossing projections were only small and did not seem to play an important role. Recent experiments, however, showed that this separation of the tasks of the two projections may hold only for birds with frontal vision. In pigeons it was shown that the optic tectum of the tectofugal pathway receives input from all over the retina, whereas the input to the n. opticus principalis thalami (OPT) of the thalamofugal pathway comes mainly from the central

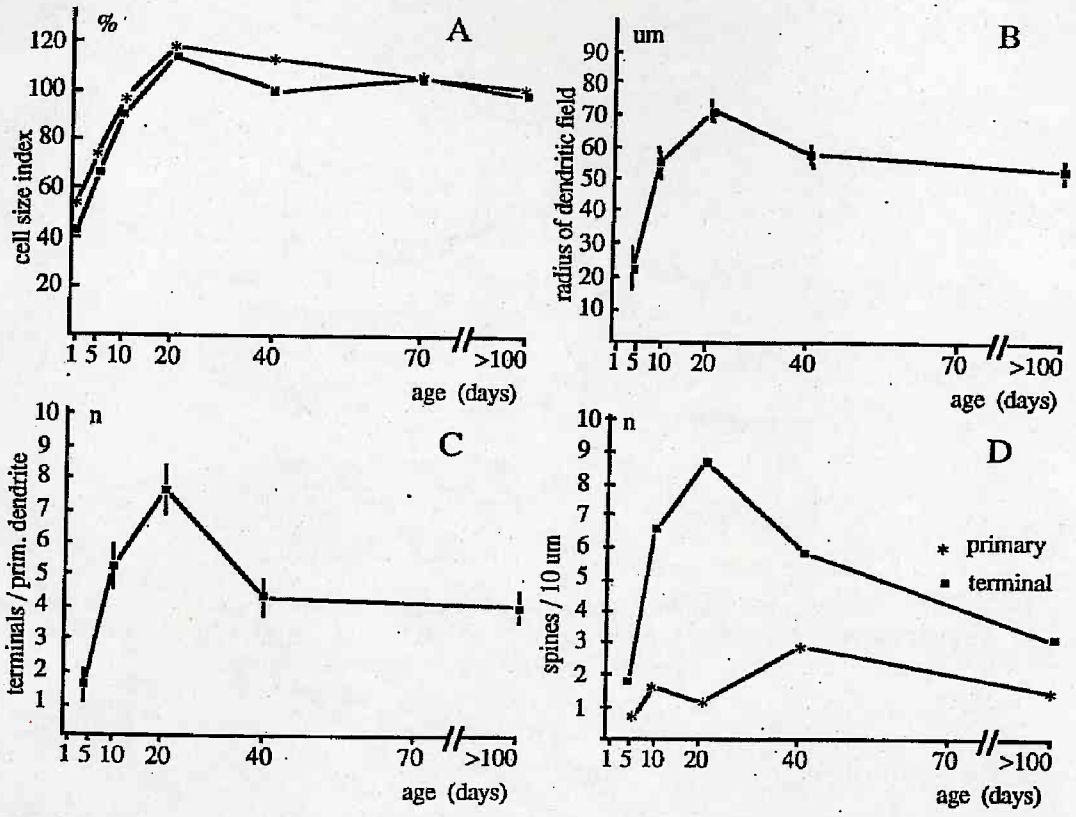

Fig.2. Time course of development of different neuronal elements. a: neuron size in % of the adult values. Stippled line: ectostriatum, full line: n. rotundus. After Herrmann and Bischof (1986a). b-d: ectostriatal measurements. b: average radius of the dendritic field, c: number of terminal segments per primary dendrite, d: number of spines / micrometer for different segments of the dendrite. Primary: segments directly adjacent to the cell body, terminal: end segments of each dendrite. After Herrmann and Bischof (1988b).

retina, which does not contribute to binocular processing in laterally eyed birds because of the large divergence of the eyes (Remy and Güntürkün 1991). Our own studies (Bredenkötter and Bischof 1991) show that the visual wulst in zebra finches receives only minor input from the ipsilateral eye and is accordingly not very likely to be involved intimately in processing of binocular images. We also showed that the recrossing projections within the tectofugal pathway are more prominent than previously believed (Bischof and Niemann 1990), and that a substantial amount of information from the ipsilateral eye is reaching the ectostriatum (Engelage and Bischof 1988, 1989). We therefore propose that in laterally eyed birds information from the binocular part of the visual field is more likely to be processed by the tectofugal pathway.

DEVELOPMENT OF THE TECTOFUGAL PATHWAY

We investigated the development of two of the nuclei of the tectofugal pathway, the nucleus rotundus and the ectostriatum, with light- and electron microscopic methods (Herrmann an 1988a,b, Nixdorf and Bischof 1986,1987). Our data clearly show that the two nuclei seem to develop almost in parallel. Fig. 2. summarizes the data we obtained from light microscopic studies. Fig. 2a (Herrmann and Bischof 1986a) shows the development of neuron size in the nucleus rotundus (solid line) and the ectostriatum (stippled line), as determined by measuring the area of the neurons in Nissl-stained sections with help of a graphics tablet. The next three figures (Herrmann and Bischof 1988b) depict the development of the main type of ectostriatal neurons as revealed by the Golgi method: the radius of the dendritic field measured from the center of the cell body to the most peripheral terminal end of a dendrite (fig.2b), the number of terminals (i.e. free endings) per

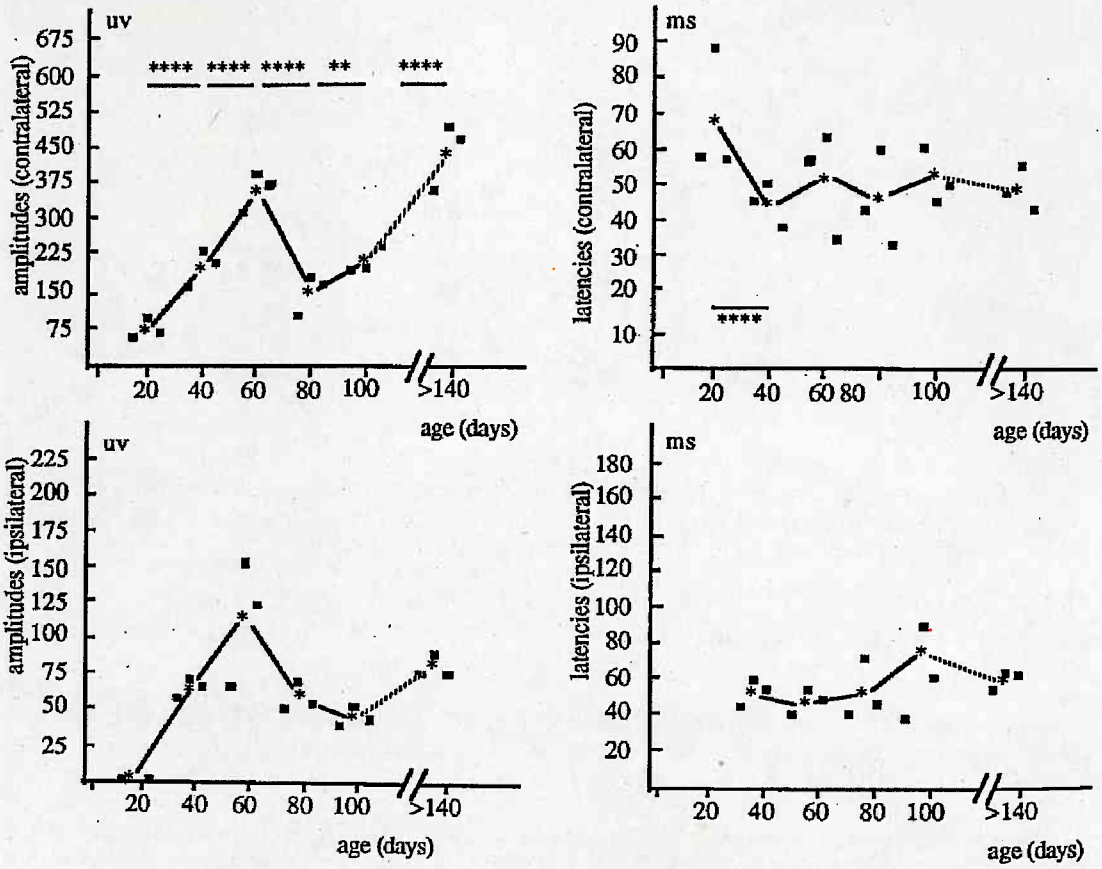

Fig. 3. Time course of development of contralaterally (upper graphs) and ipsilaterally (lower graphs) visually evoked potentials in the ectostriatum of the zebra finch. Left side: amplitudes, right side: latencies. Open circles: means (+- SEM) of individual birds. Closed circles: means (+- SEM) of pooled data from three birds each. Significance levels: ++++ = $p<.00001$, +++ = $p<.0001$, ++ = $p<.001$ (two tailed Student's T-test). No significant difference ($p>.05$) in all other cases. From Engelage and Bischof (1991).

primary dendrite (fig.2c) and the number of spines/10 µm dendritic length measured at different segments of the dendritic tree (fig.2d).

All light microscopically investigated parameters increase very rapidly from day 5 after hatching to day 20, the increase being most drastically between day 5 and day 10. All measurements show a peak at day 20 and a subsequent significant decrease between day 20 and 40.

In contrast to the data obtained by light-microscopic methods, the patterns obtained by measuring ultrastructural parameters of neurons such as length of the postsynaptic thickening, the size of the presynaptic terminal, and the number of synapses per square unit during development were not as clear-cut. Whereas the synaptic measurements in general showed an increase until day 20, a decline, as observed between day 20 and day 40 in the light microscopic studies, was only very small or even absent in the measurements of ultrastructural features of n. rotundus as well as of ectostriatum neurons (Nixdorf and Bischof 1986, Nixdorf 1990).

Despite of these differences, which will be discussed later, the data allow to conclude that the morphological development of the nucleus rotundus and the ectostriatum is almost complete at about day 40. This does not hold for the physiological development of the ectostriatum. Our measurements of visually evoked responses within this nucleus clearly demonstrate that the

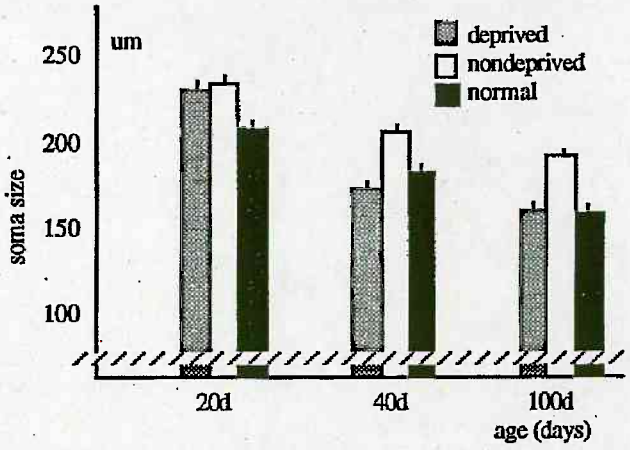

Fig. 4. Effects of different times of monocular deprivation (20, 40, and 100 days from birth) on neuron size of n. rotundus. Deprived, nondeprived: see fig. 1, normal: values from birds raised without deprivation. After Herrmann and Bischof (1988b).

response properties of the ectostriatum are still changing even when the birds are older than 100 days.

As stated earlier, studies from our lab (Engelage and Bischof 1988, 1989) demonstrated that the ectostriatum receives, contrary to earlier prepositions, input from the ipsilateral as well as the contralateral eye. The ectostriatal response evoked by a flashing light (visually evoked potential, VEP) directed to the ipsilateral eye (ipsilateral VEP) is much smaller than that evoked by stimulation of the contralateral eye (contralateral VEP). As can be seen in fig. 3 (Engelage and Bischof 1990), the development of the amplitudes and latencies follows a similar course for either side, but with a delay of about 20 days for the ipsilateral response. The amplitudes of the contralateral VEP's are still very low at day 20 (the earliest developmental stage where stereotaxic access and recording from the ectostriatum was possible) and ipsilateral VEP's are even absent (below noise level). A sharp increase can be observed between day 20 and day 60, followed by a steep decrease until day 80 with contralateral and day 100 with ipsilateral stimulation. Beyond these ages, the amplitudes are rising again, reaching constant levels at about day 140 to day 160.

A shortening of latencies is observed between day 20 and day 40 with stimulation of the contralateral eye, most probably due to myelination of axons, which is adult-like with 40 days (Herrmann and Bischof 1986a). Thereafter, latencies remain at a constant level with contralateral stimulation.

PLASTICITY OF THE TECTOFUGAL PATHWAY

We addressed the question of how the morphological development of the n. rotundus and the ectostriatum is altered by changes of visual experience during development by monocularly depriving the birds for different times starting shortly after hatching, before natural eye opening, and sacrificing them at the end of the deprivation period. Fig. 4 (Herrmann and Bischof 1986c) demonstrates that on neurons of n. rotundus this treatment has different effects according to its duration. After deprivation of 20 days starting shortly after birth there is an increase in cell size of the neurons of both hemispheres, the one driven by the deprived eye as well as that driven by the nondeprived eye, if compared to values obtained in normally reared birds. Deprivation for 40 or 100 days causes a significant hemispheric difference in soma size: neurons of the deprived n. rotundus are 15 % smaller than those of the nondeprived side. This difference is not due to a shrinkage of the neurons on the deprived side, as one would expect, but rather a result of a hypertrophy of the neurons on the nondeprived side, as can be seen by comparison with measurements of normally raised animals of the same ages.

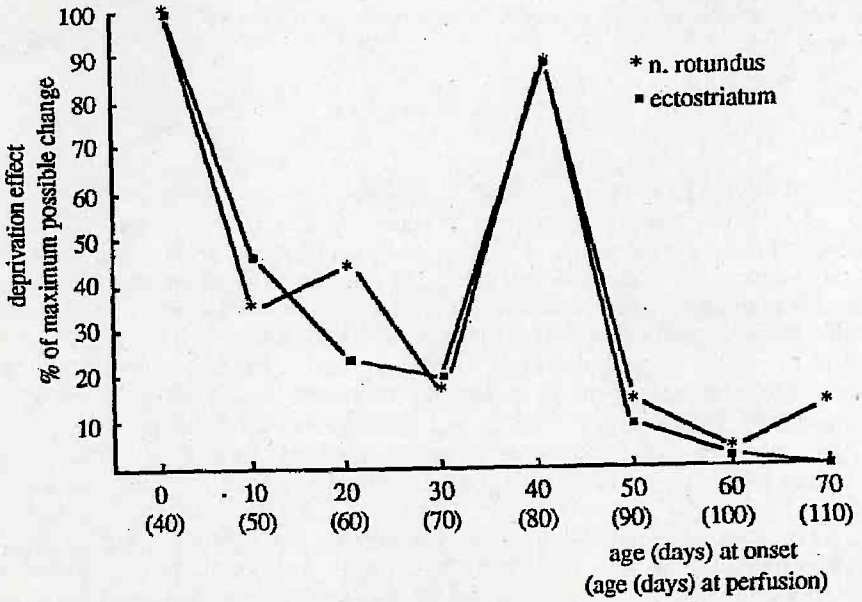

Fig. 5. Sensitive period for the effects of monocular deprivation derived from left-right differences of neuron size in the ectostriatum and n. rotundus of monocularly deprived birds. The difference between the hemispheres of birds deprived for 40 days from birth was set to 100 %. After Herrmann and Bischof 1988a).

Whereas the same effects can be observed in the ectostriatum (Herrmann and Bischof 1986b), no comparable changes of neuronal morphology could be observed in peripheral stations of the visual pathway. Monocular deprivation does not have any significant effect on the size of the retinal ganglion cells, independent of deprivation time. Within the optic tectum, the effects seem to be different for the different layers: No effect could be observed in layer 5 which receives the axons of the retinal ganglion cells. Neurons of layer 13, however, which send their axons to n. rotundus, were smaller in the deprived than in the nondeprived hemisphere. These results clearly show that effects of monocular deprivation become more pronounced in central compared to peripheral areas (Herrmann and Bischof in prep.).

Our results concerning the ultrastructural effects of monocular deprivation on n. rotundus and ectostriatum neurons are less clear-cut (Nixdorf and Bischof 1987, Nixdorf 1990). A finding comparable to our light microscopic studies was that both hemispheres are affected by 20 days of monocular deprivation which started shortly after hatching. However, in contrast to cell size and spine density, measurements of the number of synapses as well as the size of the presynaptic terminal and the length of the postsynaptic density of ectostriatal neurons resemble closely those of normally reared birds if deprivation is maintained for 100 days from birth.

Another study of our lab (Herrmann and Bischof 1988a) demonstrated that the effect of monocular deprivation is critically dependent on the time of the onset of the deprivation period. To determine this, cell size was measured within the right and left n. rotundus and ectostriatum in birds subjected to 40 days of monocular eye closure starting at ages regularly spaced throughout the first 70 days of age. Fig. 5 shows the difference of neuron size between the deprived and the nondeprived hemisphere, respectively, of the different age groups. It demonstrates that monocular deprivation causes marked differences in neuron size in n. rotundus and ectostriatum if the treatment starts at hatching. Starting deprivation between 10 and 80 days of age results in a progressively smaller difference between the two hemispheres with one surprising exception: If deprivation started at day 40, a second sharp increase of hemispheric differences was observed (fig.5).

These data indicate that the sensitivity of both rotundal and ectostriatal neurons for changes of the visual environment is extremely high shortly after birth and a second time at an age between

40 and 80 days, when our morphological measurements indicated that normal development is almost finished.

DISCUSSION

Our light microscopic measurements of the development of the tectofugal visual pathway clearly demonstrate that neurons grow rapidly until day 20. Thereafter, the size of neurons and complexity of neuronal elements such as spines and dendrites decreases until day 40, reaching adult values in most cases. This peak-decline trend (Murphy 1984) can be observed in a variety of animals and for many different neuronal elements (for review see Herrmann and Bischof 1988b). Most theories of brain development argue that this overproduction of neuronal elements is due to the fact that it is not possible for the genetic program to precisely define the structure of the neuronal network for optimal processing of environmental stimuli. Therefore, a redundant network is built which is shaped to its final form by a selection process ("selective stabilization") which favours functionally efficient neuronal connections over those which cannot be driven effectively by the periphery (Hebb 1949, Wiesel 1982, Changeux and Danchin 1976).

Our electron microscopic data do not show the substantial decline after 20 days which was observed for example in the Golgi measures, the values instead remaining on a quite constant level after rising until 20 to 40 days of age. It is conceivable that synaptic features such as the length of the postsynaptic density and the size of the presynaptic terminal should not go down as a consequence of the process of "selective stabilization" since the efficiency of synapses should be positively correlated with the area of the postsynaptic density and the size of the presynaptic bouton. However, the number of synapses should probably show the same decrease as we demonstrated for the density of spines by the Golgi method. This has been shown to be not the case for the ectostriatum. Nixdorf (1990) demonstrated that the proportion of synapses located on spines does not remain constant during development. The percentage of synapses located on dendritic spines is reduced from 40 % in 20 day old birds to 22 % in 100 day old animals. Thus the decrease in spine density reflects, at least partly, a displacement of synapses from spines to dendritic shafts, the total number of synapses remaining constant. Whether this result is a hint against the "selective stabilization" theory, remains open to future research.

Our evoked potential studies clearly demonstrate that the physiological development of the tectofugal pathway has a delay of about 40 days compared to morphological development. This is a conceivable finding because the functioning of the ectostriatal neuronal network should be optimal when the exuberant connections, which lead to a largely random distribution of current flow vectors and a strong cancellation of currents which in turn diminishes the amplitude of the evoked potential (Llinas and Nicholson 1974, Mitzdorf 1985), are fully eliminated and the final network is stabilized.

The most surprising finding of our evoked potential studies was the sharp interruption of the linear increase in the development of the VEP amplitudes after 60 days of age. This dramatic decrease of the visual responsiveness of the ectostriatal neuronal network clearly occurs after the end of neuroanatomically detectable changes. At present, we do not have a fully conclusive interpretation for this decrease. An idea we are following up is that a second wave of progressive events occurs within the ectostriatum. Following the same line of argument already employed in the explanation of the increasing responsiveness of the ectostriatum up to 60 days, the decrease of VEP amplitudes observed at day 80 may be due to a wave of invading fibers which interfere with the originally established patterns of connectivity, leading to desynchronization of the ectostriatal network, and therefore a decrease in the VEP amplitude. This would then be followed by a second period of selective stabilization.

This view is supported by one of our findings in monocularly deprived birds (Herrmann and Bischof 1988a). We have shown that monocular deprivation affects neuronal development not equally at all ages. Instead, the sensitivity to this treatment is high for the first days after birth and, more surprising, a second time when deprivation occurs between 40 and 80 days of age.

The first peak in sensitivity has been observed in a variety of studies concerning monocular deprivation (e.g. Blakemore 1978). Most probably the neuronal tissue is more susceptible to

change of input from sense organs until the network is stabilized by selective stabilization. It has been also proposed that myelination of neuronal tissue limits the capability of neurons to undergo alterations (LeVay and Stryker 1979). Myelination is adultlike in the zebra finch visual system with about 40 days of age (Herrmann and Bischof 1986a).

Thus, the drastic effect of monocular deprivation in zebra finches deprived for 40 days from hatching may be due to low myelination and hence more impact of selective stabilization mechanisms during early development. However, with 40 days of age the myelination of ectostriatal neurons is complete; nonetheless, there is a second peak in monocular deprivation effects if deprivation starts at this time. At present we prefer to relate this finding to the electrophysiological results which show a depression of ectostriatal responses after 60 days of age: Both results may indicate a second phase of reorganization of ectostriatal connectivity, probably induced by invasion of new fibers. Experiments to examine this idea are underway.

Finally, we want to discuss another result of our deprivation studies which shows that the effects of monocular deprivation in the tectofugal pathway of birds can clearly be compared to findings concerning the visual cortex of mammals.

In cats as well as in monkeys the most drastic effects of monocular deprivation can be detected on neurons receiving binocular input. The only effect seen in monocularly driven neurons, as for example in the monocular segment of the lateral geniculate nucleus of the cat (Cragg et al.. 1975), was a minor shrinkage of neurons and neuronal elements. When starting our experiments we expected to find only small effects because of the proposed "monocular nature" of the tectofugal pathway. In contrast, our results indicate that the two hemispheres interact in the reaction to monocular deprivation.

In some cases, the nondeprived hemisphere obviously enhances the size of neurons and number of neuronal elements, perhaps in order to compensate for the lack of input of information to one eye by enlarging the stimulus processing capacities of the intact hemisphere. Most probably, the interaction of the two sides implies some sort of competition process between the two visual inputs, as demonstrated for the development of visual cortex neurons in mammals (rev. Fregnac and Imbert 1984). One has to note, however, that the process may not be fully comparable because zebra finches are birds with a very small binocular field. Interestingly, in mammals with laterally placed eyes like rabbits (Chow and Spear 1974) or in the monocular LGN segment of cats (Hickey et al.. 1977) no substantial deprivation effects (except small shrinkage of LGN neurons as a direct consequence of deprivation) could be observed.

The idea that competition mechanisms contribute to the observed effects is supported by our findings (Herrmann and Bischof in prep.) that in retinal ganglion cells and in layer 5 of the optic tectum no effect is observable. Both neuron populations are monocularly driven. The effects found in layer 13 of the optic tectum can already be interpreted as a sign for binocular interaction, because a tecto-tectal projection has been described (Robert and Cuenod 1969).

In addition to the indirect evidence provided by our deprivation studies we have directly demonstrated that areas of the tectofugal systems of both hemispheres are heavily interconnected. Injections of the anterograde tracer 3H-proline into the tectum and of the retrograde tracers RITC and HRP into the n. rotundus revealed that the interhemispheric connection between these two areas are much more massive than previously believed Bischof and Niemann 1990). This was confirmed by an electron microscopic study of lesion- induced degeneration (Bischof and Brinkkötter in prep).

Taken together with our electrophysiological findings which demonstrate that the ectostriatum processes ipsi- as well as contralateral stimuli (Engelage and Bischof 1988,1989), these results suggest that the tectofugal pathway is not, as previously believed, a monocularly driven pathway, but is capable to process binocular information as well. Therefore, our studies support the view that the tectofugal pathway has many characteristics of the geniculocortical pathway of mammals, although the two structures are not homologues.

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