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Enucleation enhances ipsilateral flash evoked responses in the ectostriatum of the zebra finch (Taeniopygia guttata castanotis Gould)

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Summary. The tectofugal pathway in birds has been reported to process primarily information from the contralateral eye. Although this pathway has access to the contralateral hemisphere by various connections, electrophysiological recordings up to now have failed to demonstrate any excitatory influence of visual stimulation in the higher stations of this pathway. This study is the first to demonstrate an excitatory projection from the ipsilateral eye to the telencephalic projection area of the tectofugal pathway by recordings of visually evoked potentials in the ectostriatum. The excitatory projection probably leads from the eye to the contralateral tectum opticum, then recrosses back to the nucleus rotundus of the ipsilateral side where it reaches the ectostriatum. In normal birds, the ipsilateral stimulus responses in the ectostriatum are smaller in amplitude and have a longer latency than responses to contralateral stimuli. In unilaterally enucleated birds, the ipsilateral response is enhanced in the ectostriatum and can be detected in the nucleus rotundus, too. The results suggest that in normal birds the ipsilateral response is inhibited to a high degree by spontaneous activity of the contralateral eye. Possibly, this counterbalanced inhibition provides a mechanism for weighting information from the left and right eye field in order to ensure adequate processing of stimuli.

Key words: Zebra finch – Visually evoked potentials – Ectrostriatum – Ipsilateral stimulus responses

Introduction

In birds, like in other vertebrates, visual information is processed by at least two different pathways (for reviews see: Cohen and Karten 1974; Emmerton 1983). The thalamofugal pathway, leading from the eye via the thalamic nucleus opticus principalis thalami (OPT) to the visual wulst, processes binocular information in spite of the fact that the optic nerve in birds crosses over completely and visual information is carried primarily to the contralateral hemisphere (Revzin 1969, 1970; Perisic et al. 1971; de Britto et al. 1975; Pettigrew and Konishi 1976; Denton 1981). Binocular processing is due to a recrossing of fibers from the OPT to the visual wulst (Perisic et al. 1971; Mihailovic et al. 1974; Bagnoli and Burkhalter 1983).

In contrast, the tectufugal pathway, which leads from the eye to the tectum opticum of the contralateral side, then to the nucleus rotundus of the thalamus and to the ectostriatum of the telencephalon, has been considered to be an almost exclusively contralaterally driven projection (Revzin and Karten 1966/1967; Parker and Delius 1972; Mori 1973; Nixdorf and Bischof 1982). Ipsilateral projections of the eye, which have been described in several studies, seem to be lost almost totally soon after birth (McLoon and Lund 1982; O'Leary et al. 1983), and the few remaining fibers apparently do not make synapses in the tectum (Bons 1976; Mc Loon 1982; O'Leary et al. 1983; Takatsuji et al. 1983). As yet, no influence of ipsilateral eye stimulation has been reported for any station of this patwhay in birds. Electrophysiological evidence for hemispheric interaction within this pathway was provided by Robert and Cuenod (1969a, b), who demonstrated that the tecti optici of the two sides inhibit each other via the decussatio supraoptica (DSO) and commissura posterior (CO). Hardy et al. (1984) demonstrated that EPSP's and IPSP's can be recorded intracellularly after electrical stimulation of the opposite tectum.

As the tectufugal pathway is by far the most prominent one in birds with lateral eyes like the

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Offprint requests to: H.-J. Bischof (adress see above) zebra finch, we suspect that this pathway is of major importance for the processing of visual information in these birds. As panoramic vision obviously cannot be perfect without interhemispheric communication, we could not believe that this tectal interaction is the only possibility of information transfer between both sides of the tectofugal pathway.

No information is available on the influence of ipsilateral stimuli on higher stations of the tectofugal pathway. A connection between the tectum opticum and the nucleus rotundus of the contralateral side has been found by anatomical methods. Although this projection has been described to be minor (Benowitz and Karten 1976; Hunt and Künzle 1980), it should have some influence on the processing of ipsilateral stimuli. Moreover, projections from the binocularly driven visual wulst of the thalamofugal pathway to the ectostriatum of the tectofugal pathway have been demonstrated (Karten et al. 1973; Nixdorf and Bischof 1982; Watanabe et al. 1985). Bagnoli et al. (Bagnoli et al. 1980) demonstrated a direct bilateral connection from the visual wulst to superficial and deeper layers of the tectum opticum. Again, these projections should have influence on the processing of visual information in the tectofugal pathway. Field potential and single unit recordings following electrical stimulation of the visual wulst demonstrate, that this influence on the tectum is mainly inhibitory, although some wulst driven units in the tectum opticum show excitatory reactions (Bagnoli et al. 1977; Bagnoli et al. 1979).

To examine such influences, we recorded visually evoked potentials (VEPs) from different relay stations of the tectofugal pathway with ipsi-, contra- and bilateral stimulation in normal birds. We also recorded from unilaterally enucleated birds for two reasons: Firstly, ipsilaterally evoked potentials in normal birds might have been artifacts due to light spreading from the stimulated eye to the nonstimulated eye (Ehrlich and Mills 1985). Secondly, the results of Robert and Cuenod (1969a, b) and Hardy et al. (1984) demonstrate that at least part of the influence between the hemispheres is inhibitory instead of excitatory. This inhibition should be reduced by unilateral enucleation.

Material and methods

The experiments were performed on 30 adult male and female zebra finches. Three of the birds (one female and two males) were enucleated unilaterally. In two cases we removed the right eye, in one the left one. The recovery periods between enucleation and electrophysiological measurements was three days, one week, or three weeks, respectively. For enucleation, the birds were anaesthetized with equithesin (0.05 ml). The eye was removed after additional local anaesthesia with novocaine.

For electrophysiology, the birds were anaesthetized with urethane (20% w/v, 0.1 ml) and mounted in an especially designed stereotaxic headholder (Bischof 1981). Evoked potentials were recorded with glass microelectrodes filled with Alcian blue in 3 M NaCl (5–15 MΩ). In each experiment with normal birds, recordings were made from one or two of the three main stations of the tectofugal pathway, the tectum opticum, nucleus rotundus and ectostriatum. In the enucleated birds, all three areas in both hemispheres were investigated successively in each experiment. The stereotaxic coordinates for the electrode positions were derived from an atlas of the zebra finch brain (Bischof and Nixdorf, unpublished).

Visual stimuli were provided by a stroboscope. Flashes were directed to one or both eyes by a fiber optics system which could be controlled by shutters. The terms ipsilateral and contralateral refer to the position of the recording electrode. In the case of bilateral stimulation, we stimulated both eyes simultaneously. Controls were made by closing the shutters in the fiber optics system or, in some cases, by removing the fiber optics system from the eyes.

Signals were averaged 64 times by a Nicolet Signal Averager. Storing and processing of the data was accomplished by a HP-86 microcomputer. This device also triggered the stimuli and controlled the experimental procedure. Amplitudes and peak latencies were estimated with a minimum – maximum routine of the computer. In addition, detailed information on amplitudes and latencies was obtained by processing the evoked potential plots on a graphics tablet.

As a control, few-unit activity was measured with different filter properties with the same experimental setup.

Differences between both hemispheres and ipsi- and contralateral stimuli were tested by a two tailed Student's t-test and a two tailed Mann-Whitney U-test.

Results

Normal birds

Concerning contralateral stimulation in normal birds we were able to confirm the results of Mori (1973) and Holden (1968a, b) for the tectum opticum and Revzin and Karten (1966/1967) for the nucleus rotundus and ectostriatum of the pigeon. Tectal VEPs evoked by contralateral stimulation are characterized by several sharp negative-positive waves, with latencies around 18 ms for the first peak (Fig. 1). The contralaterally evoked VEPs of the nucleus rotundus are characterized by a single positive wave with one or two distinct peaks with latencies between 25 and 30 ms for the first peak (Fig. 1).

Potential shape and latency of contralateral rotundus and ectostriatum recordings (Fig. 1) are in good agreement with previous studies (Revzin and Karten 1966/1967; Parker and Delius 1972). Contralateral stimulus responses of the ectostriatum are mainly characterized by a slow negative-positive wave superimposed by several sharp spike like peaks. The latencies of the ectostriatal VEPs evoked contralaterally varied, between 40 and 70 ms. This was clearly dependent on the site of the recordings. The

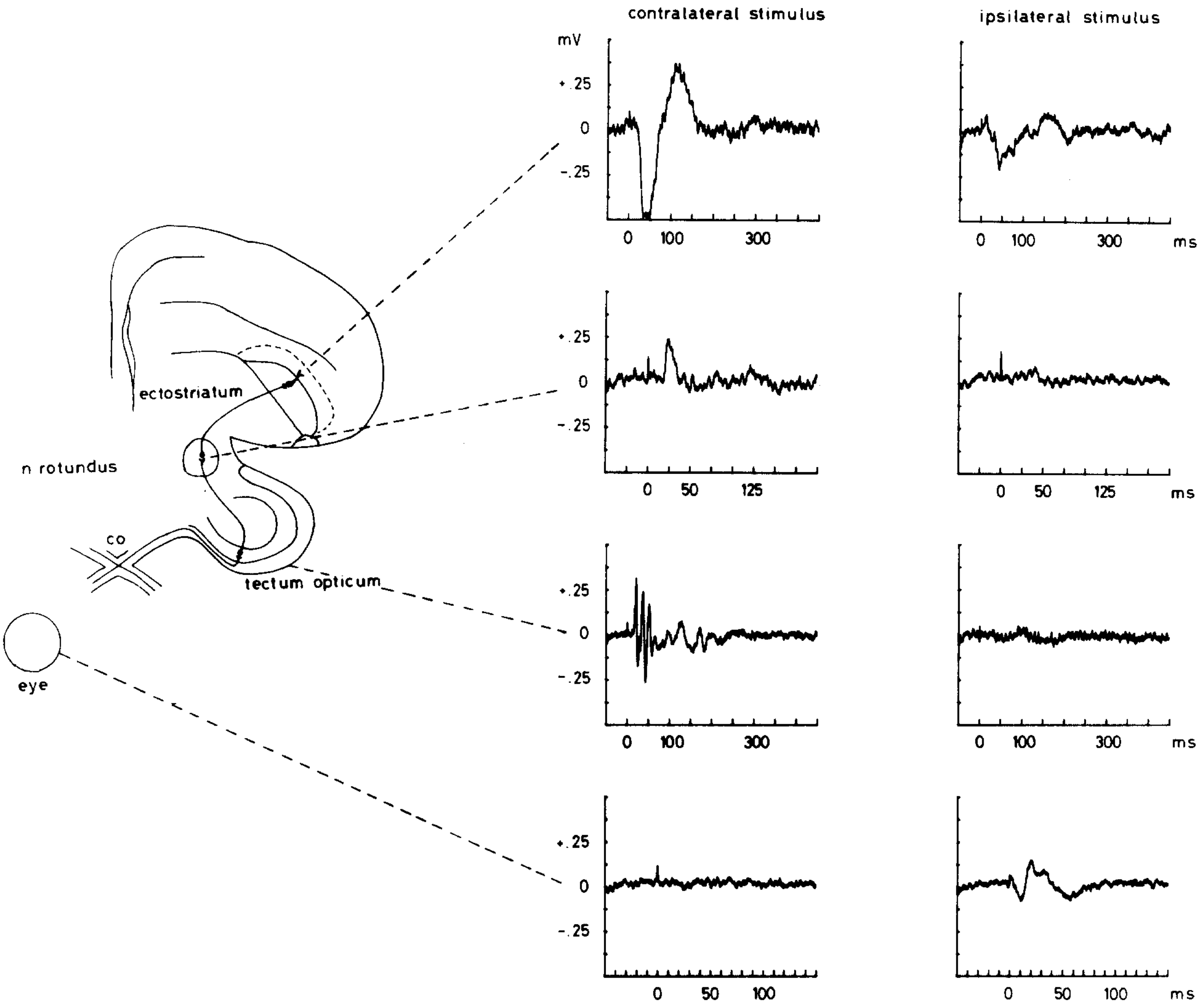

Fig. 1. Averaged VEPs from the tectofugal pathway of the zebra finch. Left: simplified diagram of the pathway. Right: diagrams from top to bottom: Recordings from ectostriatum, nucleus rotundus, tectum opticum and contralateral eye. Left column: contralateral stimulation; Right column: ipsilateral stimulation. Average 64 ×, bin width between 200 and 500 μs (see variations of the time scale), stimulus at 0 ms

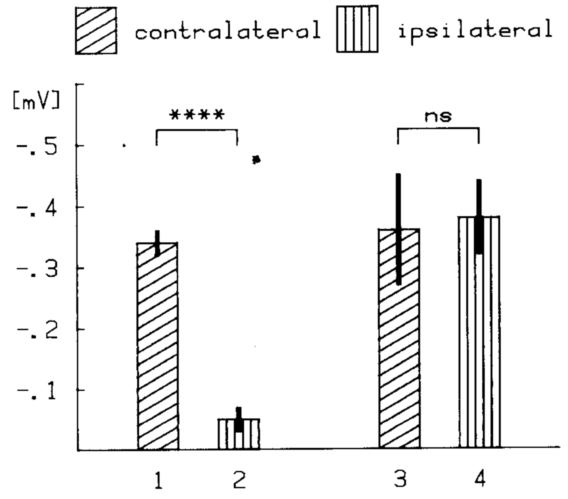

Fig. 2. Means of amplitudes and standard errors of the mean of contra- and ipsilateral stimulation in the ectostriatum of normal and enucleated zebra finches. Normal birds: column 1 and 2; Enucleated birds: columns 3 and 4; ns = non significant $p > 0.2$, **** = significant $p < 0.00001$. In normal birds the amplitudes of ipsilateral responses are significantly smaller than those of contralateral responses. In enucleated birds the differences between ipsi- and contralateral responses are smaller and not significant

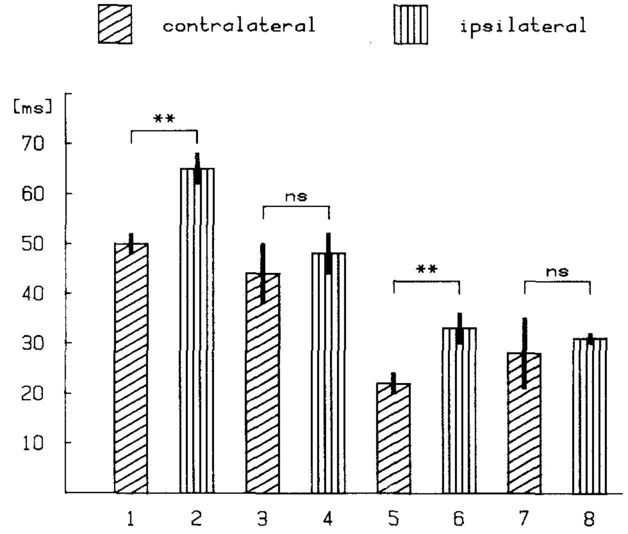

Fig. 3. Means of latencies and standard errors of the mean of contralateral and ipsilateral stimulation in the ectostriatum of normal and enucleated zebra finches. Columns 1, 2 peak latencies in normal birds, columns 3, 4 peak latencies in enucleated birds, columns 5, 6 latencies of the first deflections in normal birds and columns 7, 8 latencies of the first deflections in enucleated birds. ns = non significant $p > 0.2$, ** = significant $p < 0.001$. All latencies of ipsilateral responses are longer than those of contralateral responses. In enucleated birds the differences are smaller and not significant

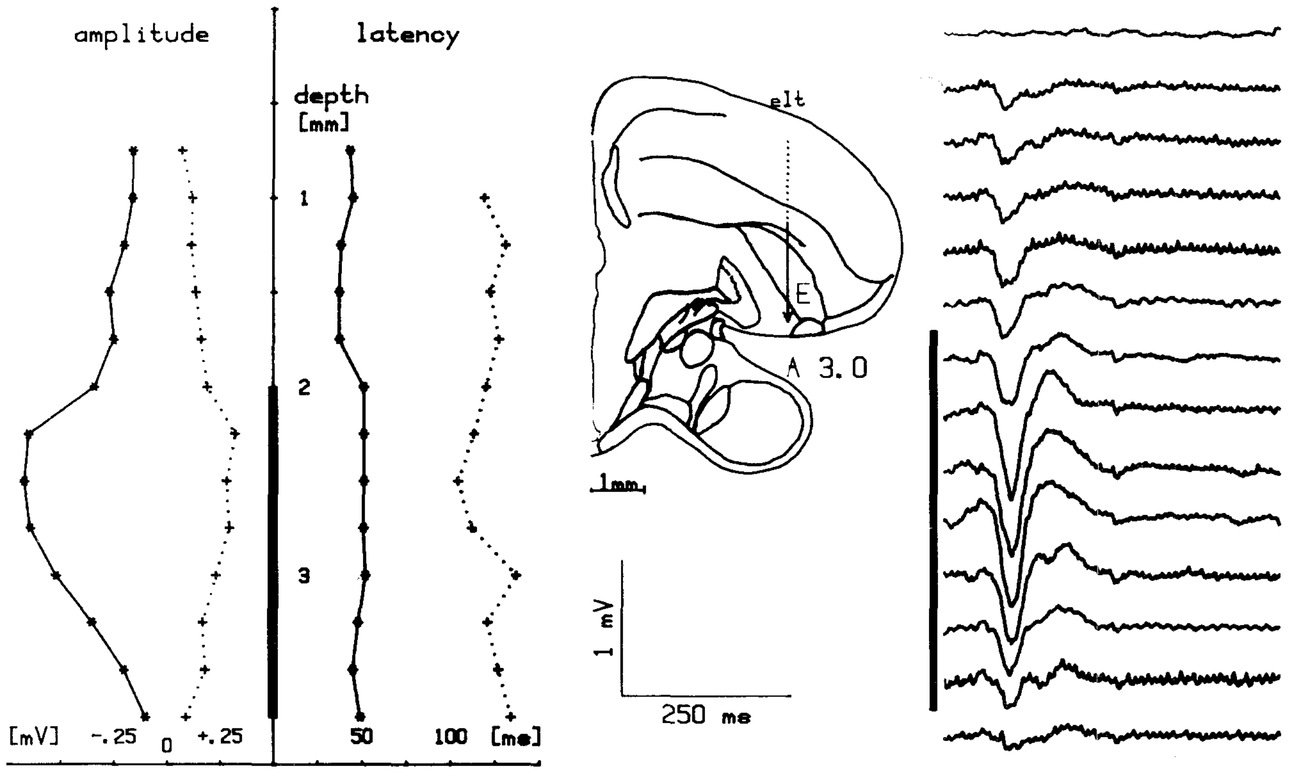

Fig. 4. Averaged VEPs in the ectostriatal region following contralateral stimulation. Left: amplitude and latency diagram of the negative (solid line) and positive going wave (dotted line) at different depths. Middle: frontal section of the zebra finch brain with electrode track. Right: averaged evoked potential plots along the electrode track. Step width 250 µm. The heavy bars in the left and right diagram represent the solid part of the electrode track in the middle. Note that the amplitude is largest in the ectostriatal core region

peak latency for a given coordinate remained constant and was reproducable. The amplitude of the negative-positive wave (see Figs. 1, 2) increases from the superficial hyperstriatum down to the ectostriatum, reaches its maximum within the ectostriatal core and then decreases towards the border of the telencephalon (Fig. 4). In several tracks, reversals of the negative positive wave were detected at the

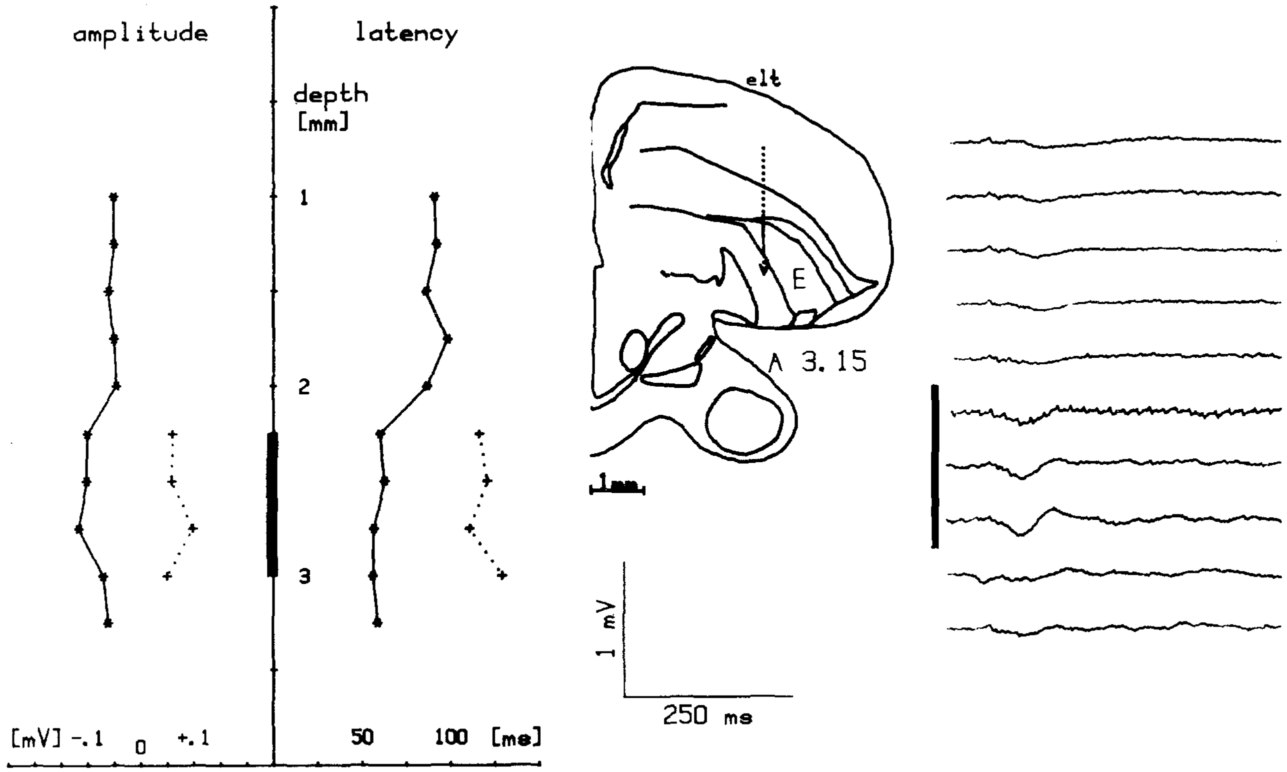

Fig. 5. Averaged VEPs in the ectostriatal region following ipsilateral stimulation. Presentation as in Fig. 4. The ipsilateral response is more restricted to the ectostriatal core region than the contralateral response (compare Fig. 4)

border of the ectostriatal core. For ectostriatum, we can clearly exclude hemispherical differences. We found no significant differences, either in amplitude or in latency of averaged evoked responses, between corresponding coordinates in the left and right hemisphere of normal birds ($p > 0.2$).

Ipsilateral stimulation never evoked reliable VEPs in the tectum opticum. Occasionally, we measured a slow positive wave with an amplitude of less than 0.01 mV and a latency of more than 100 ms in deeper layers of the tectum opticum. However, these responses could not be traced for more than 100 or 200 μm and were never clearly distinguishable from background noise. This also holds true for the nucleus rotundus.

In contrast to the tectum opticum and nucleus rotundus, reliable ipsilaterally evoked responses were demonstrated in the ectostriatum. These ipsilateral VEPs are smaller in amplitude and have longer latencies (50 ms to 70 ms) than the contra- and bilateral VEPs (Figs. 2–5) obtained at the same recording sites and are more restricted to the ectostriatal core region than the contralateral evoked responses. Ipsilaterally evoked responses normally diminish at the ventral border of the ectostriatal core (Fig. 5).

In order to minimize the probability that the measured potentials might come from another source than the ectostriatum (see discussion), we in some cases measured extracellular multi-unit activity in response to flashes. The patterns of these multi-unit recordings correspond well to the evoked potential curves (Figs. 6, 7). This demonstrates, together with a current source density analysis of ectostriatal VEPs (Engelage and Bischof in prep.) that the ectostriatum is the most likely source of the evoked responses.

Bilateral stimulation obviously does not lead to a simple summation of ipsi- and contralateral responses, as bilateral eye stimulation shows no detectable differences to contralateral eye stimulation in the ectostriatum. Addition of contra- and ipsilateral stimulus responses by the computer results in a different pattern compared to the bilateral VEPs (Fig. 8). Therefore, contralateral stimulation is suspected to suppress ipsilateral responses within the ectostriatum. This is further confirmed by the data from enucleated birds.

Enucleated birds

Stimulation of the enucleated side never elicited any VEPs in either hemisphere. This shows that the

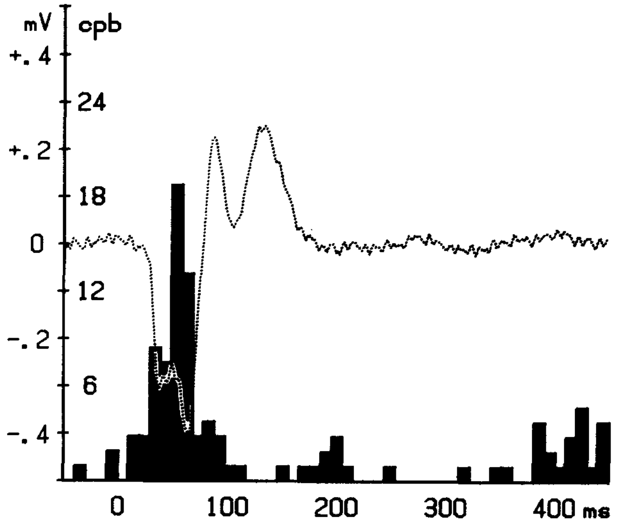

Fig. 6. Superposition of contralaterally evoked potentials and multi-unit activity at the same recording site in the ectostriatum. Stimulus at 0 ms. VEP: bin width 500 μm. Average 64 ×, ordinate scale in mV. Multi-units: bin width 10 ms. Average 16 ×, ordinate scale in counts/bin (cpb). The distribution of multi-unit activity fits well to the VEP curve

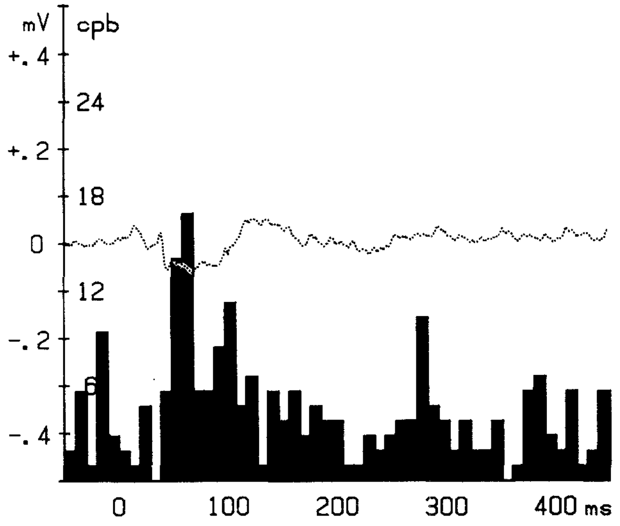

Fig. 7. Superposition of ipsilaterally evoked potentials and multi-unit activity at the same recording site in the ectostriatum. Stimulus at 0 ms. Presentation as in Fig. 6

potentials recorded ipsilaterally cannot be due to light spreading to the other eye (see discussion).

Responses to contralateral stimulation are not affected by unilateral enucleation. In the hemisphere contralateral to the remaining eye the VEPs are very similar to those obtained in normal birds. This holds true for all three relay stations (tectum opticum, nucleus rotundus and ectostriatum) of the tectofugal pathway (Fig. 9).

Ipsilateral stimulation did not elicit VEPs in the tectum opticum contralateral to the enucleated side (Figs. 10, 9). In contrast, we did obtain reliable VEPs by ipsilateral stimulation in the nucleus rotundus of enucleated birds. As described above, this was never the case in normal birds, where the occasionally occuring ipsilateral stimulus responses could never be separated from background noise. The latencies of these ipsilaterally evoked potentials were 10 to 15 ms longer than contralateral stimulus responses in normal and enucleated birds. In one bird (enucleated three weeks before the electrophysiological measurements), we detected a second positive peak with a latency of 75 ms which was not to be seen in the other enucleated and normal birds. Possibly, this is an effect of reorganization due to the longer interval between enucleation and recording (Fig. 11).

Ipsilateral VEPs recorded from the ectostriatum of unilaterally enucleated birds were dramatically enhanced compared to normal birds (Figs. 2, 3, 9). These potentials had the same amplitude as those recorded from corresponding coordinates of the other hemisphere in the same preparation with contralateral stimulation. In enucleated birds, there was no significant difference in the amplitude of contra- (–0.36 mV) and ipsilateral (–0.38 mV) evoked responses ($p > 0.2$), whereas in normal birds the difference between contra- (0.34 mV) and ipsilaterally (0.05 mV) evoked responses was highly significant ($p < 0.0001$) (Fig. 2). The peak latencies of these ipsilateral VEPs were about 5 ms longer than those of the contralateral VEPs (Fig. 3). However, the difference between contra- and ipsilaterally evoked responses decreased in the enucleated birds and was no longer significant (Fig. 3). This also holds true for the latencies of the first deflections of the negative wave (Fig. 3).

Discussion

In general, the tectofugal pathway of birds is considered to be involved mainly in processing information of the contralateral eye. Our results concerning this contralateral processing are in good agreement with a previous study (Parker and Delius 1972). Due to visual instead of electrical stimulation of the eye, the latencies obtained in this study were about ten times longer than those obtained by Revzin and Karten (1966/1967). In contrast, ipsilaterally evoked VEPs from the ectostriatum, as obtained in our experiments with normal birds, and the enhancement of ipsilateral VEPs by enucleation of the contralateral eye, have not been described before.

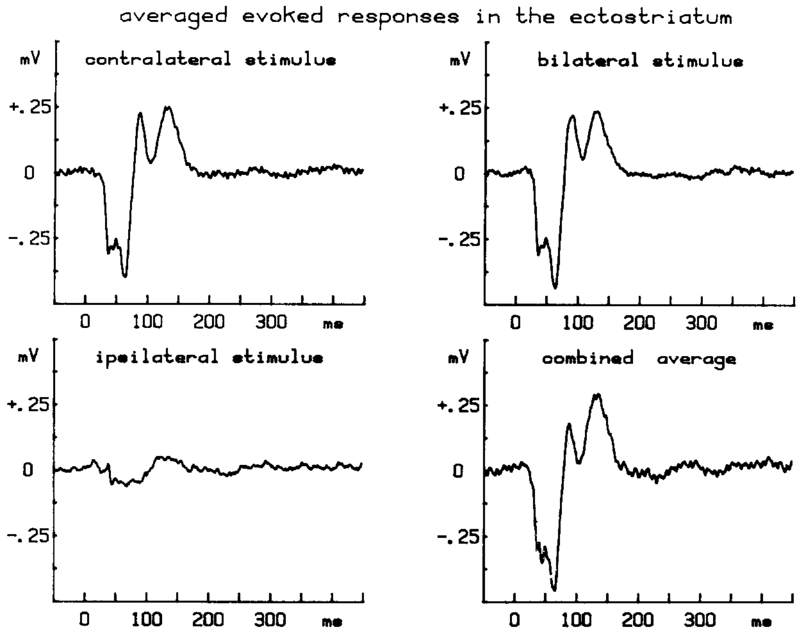

Fig. 8. Ectostriatal responses to contra-, ipsi- and bilateral stimulation. Combined average: addition of the two graphs on the left side by the computer. Note the difference between the two graphs on the right side. Average 64 ×, bin width 500 μs, stimulus at 0 ms

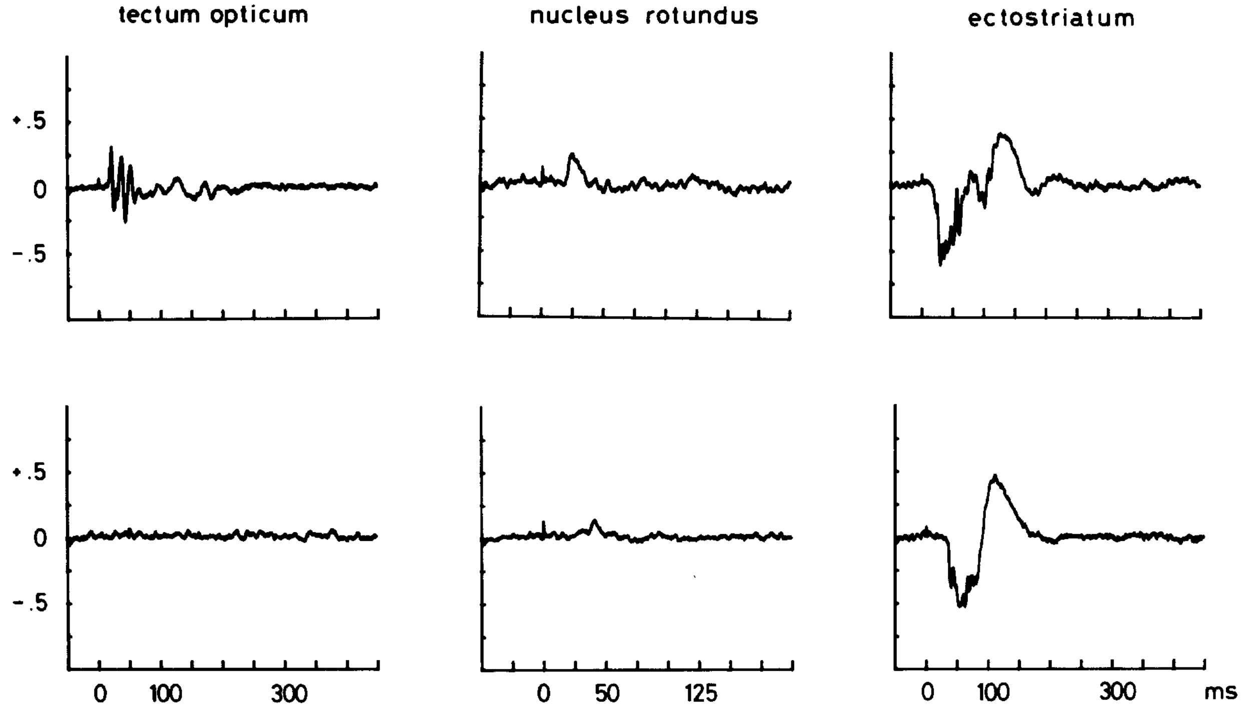

Fig. 9. Effects of enucleation on responses of three stations of the tectofugal pathway. Stimulation of the remaining eye shows no alteration of responses in the contralateral hemisphere (first row, compare Fig. 1). Ipsilateral responses are enhanced in nucleus rotundus and ectostriatum, not in tectum opticum (second row compare Fig. 1). Recordings from the bird enucleated three days before the electrophysiological experiment. Ordinate scale in mV

Before we started to record from unilaterally enucleated birds, we had some doubts, whether the ipsilateral stimulus responses were the result of a real ipsilateral projection. Two possibilities of artifacts have to be considered. First, there may be some light spreading directly from the fiber optics to the non-stimulated eye. Second, the contralateral eye may be stimulated indirectly through the stimulated eye

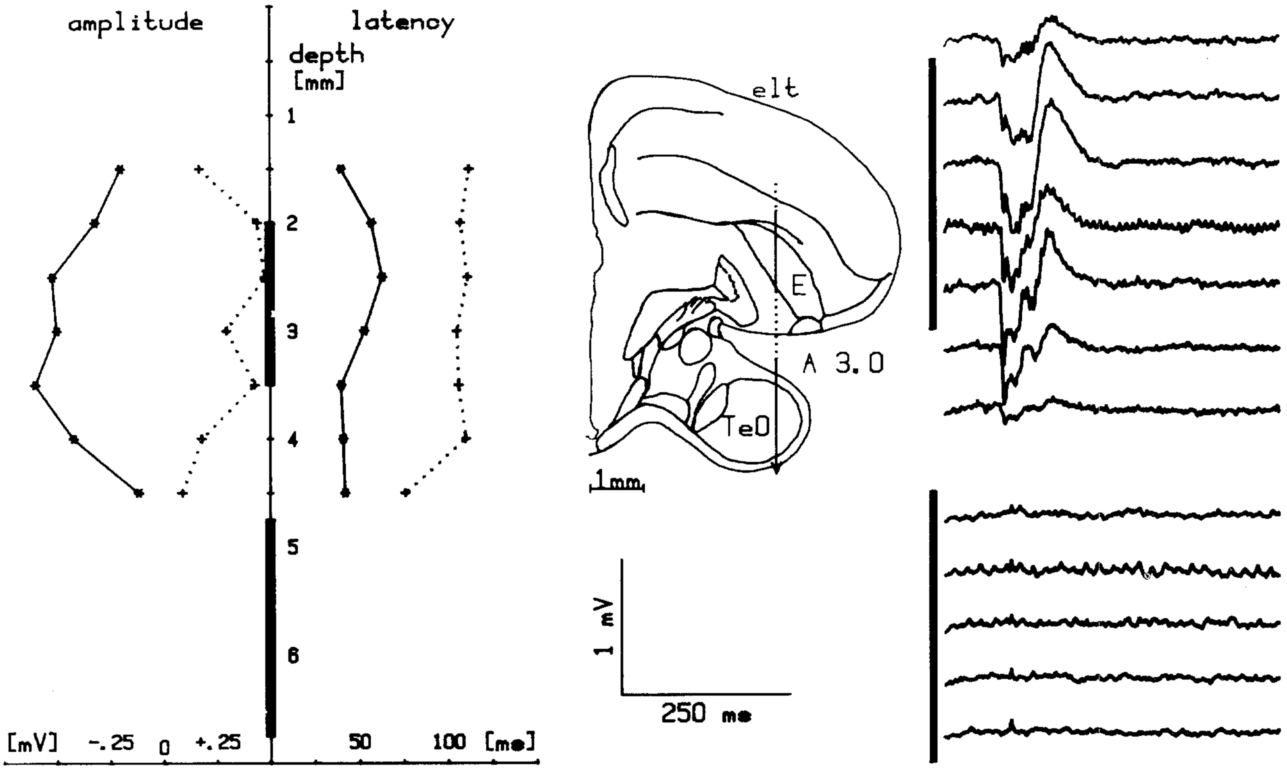

Fig. 10. Averaged ipsilateral VEPs in the ectostriatum and tectum opticum of an adult enucleated bird following stimulation of the remaining eye. Presentation as in Fig. 4. Note the enhanced ipsilateral evoked response (compare Figs. 4, 5 and 10) and the lack of tectal VEPs

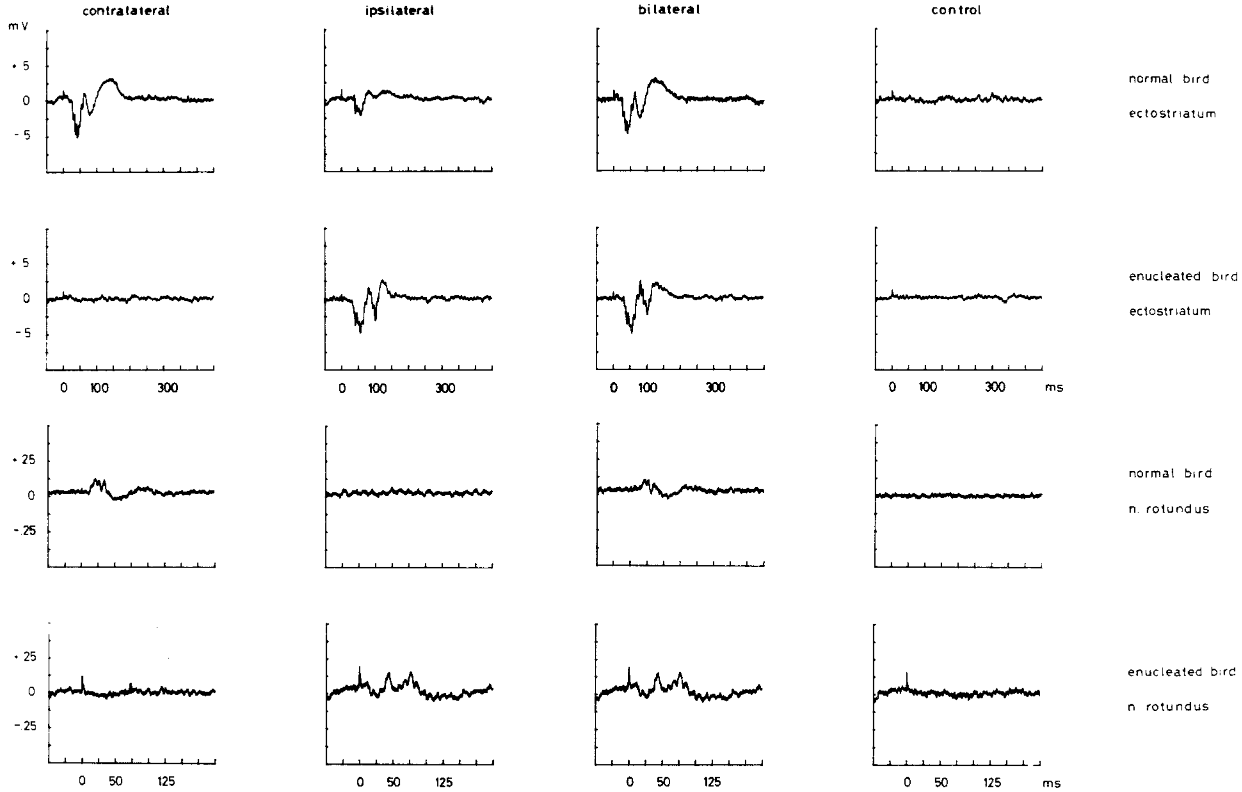

Fig. 11

via the lightpermeable cartilaginous membrane (interocular septum), which separates the two eyes (Ehrlich and Mills 1985). In both cases stimulation of the eye ipsilateral to the recording site would simultaneously stimulate the contralateral eye with reduced stimulus intensities. From other experiments (Engelage and Bischof in prep.), we have indications that reducing the intensity results in a reduction of the amplitude and an increase in the latency, effects which are also obtained with ipsilateral stimulation. Our recordings from enucleated birds, however, indicate that spreading of light cannot be the stimulus for the ipsilaterally evoked visual responses.

Another source of artifacts often considered in evoked potential studies is the passive spreading of potentials from one area to another. In this case the VEP response would give no reliable information on the localization of its source. Although this is a more severe problem in studies with electrical stimulation, we have at least four arguments which make it likely that the VEPs described above are detected at their source: First, we found clearly distinguishable and characteristic evoked responses in all three relay stations of the tectofugal pathway, indicating that we really recorded VEPs from three different sources. Second, in ectostriatum and nucleus rotundus, potentials became smaller towards the periphery of the nuclei. Third, in some cases we found a reversal of the evoked potential waves which clearly demonstrates that we had gone through the source. Fourth, we can show for the ectostriatum and nucleus rotundus that the few-unit responses we recorded are in good agreement with the evoked potentials. This proves that the EPs are really evoked by the neuronal activity of this area and ensures that the information on the localization of the evoked potential sources is reliable.

Therefore, our recordings undoubtedly demonstrate that the ectostriatum receives contra- as well as ipsilateral excitatory projections. Moreover, they give information on the pathway by which this ipsilateral influence is processed and about the nature of the binocular interaction in the tectofugal visual pathway of the zebra finch.

In view of their long latency of more than 100 ms the occasional ipsilateral tectal VEPs can be excluded as a trigger for the ipsilateral ectostriatal responses. It is more likely that these very sluggish responses are due to the inhibitory influence from the visual wulst to the tectum opticum (Bagnoli et al. 1979). It is unlikely that our failure to demonstrate other, more reliable ipsilateral VEPs in the tectum opticum is due to improper experimental prodecures. We recorded contralateral VEPs from the tectum opticum following each ectostriatum penetration with the same electrode. The tectum tracks involved superficial as well as middle and deeper layers in both the normal and the enucleated birds. It is unlikely that we have overlooked some potentials which are principally detectable with our method. Therefore, the excitatory influence mediated by the tecto-tectal commissure (Hardy et al. 1984) obviously has not a prominent effect on the overall tectal response.

We instead suggest that ipsilateral visual information is conveyed from the ipsilateral eye to the contralateral tectum opticum, then recrosses back to the ipsilateral nucleus rotundus and terminates in the ectostriatum of the same side, as these are the stations of the tectofugal pathways in which we detected VEPs evoked by ipsilateral stimulation in enucleated birds. There is also anatomical evidence for such a projection (Benowitz and Karten 1976; Hunt and Künzle 1976; Bischof and Niemann in prep.). Likewise, it may be possible that the n. subpraetectalis (SP) and the n. interstitio-praetecto-subpraetectalis (IPS), which receive information from the contralateral tectum (Hunt and Künzle 1976) and project to the n. rotundus (Benowitz and Karten 1976) are involved in the processing of the ipsilateral influence.

The comparison of the different stimulus combinations (Fig. 2) clearly demonstrates that the effect of contra- and ipsilateral stimulation is not additive. In normal birds, the excitatory influence on the ipsilateral side seems to be inhibited to a large degree, as ipsilateral responses are not detectable in the nucleus rotundus of normal birds, and ipsilateral VEPs from the ectostriatum are much smaller in amplitude in normal than in enucleated birds. It is likely that this inhibition is already maintained by the spontaneous activity of retinal ganglion cells or at least by very low stimulus intensities, as only these parameters are affected by enucleation of the eye.

Single cell recordings in the tectum opticum of the pigeon (Robert and Cuenod 1969a, b; Hardy et al. 1984) indicate such inhibitory interactions

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Fig. 11. Summary of the effects of enucleation on responses of the ectostriatum and nucleus rotundus. Data from the bird enucleated three weeks prior to the experiment. Alterations occur for ipsilateral responses of ectostriatum and for ipsi- and bilateral responses of nucleus rotundus. Stimulation of the enucleated eye elicits no responses on the contralateral side (first column). Alterations due to enucleation can be observed for ipsilateral stimulation in both nuclei (second row), for bilateral stimulation in the nucleus rotundus (third row). Bin width 500 μs for ectostriatum, 250 μs for nucleus rotundus and tectum opticum

between the two tecti optici in normal birds. This inhibition at the tectal level might lead a to suppression of ipsilateral responses in the subsequent stations of the pathway, the nucleus rotundus and the ectostriatum. The possibility of inhibitory influences of the tectum opticum on the contralateral nucleus rotundus or rotundus-rotundus interactions, however, cannot be excluded yet. Mihailovic et al. (Mihailovic et al. 1974) demonstrated such interactions between the thalamic nuclei of the OPT complex in the thalamofugal pathway of birds.

Moreover, the wulst-tectum projections (Bagnoli et al. 1977; Bagnoli et al. 1979; Bagnoli et al. 1980; Bagnoli and Burkhalter 1983), which are mainly inhibitory (Bagnoli et al. 1979), have to be considered as a source of the inhibition effects. As yet we cannot explain the fact that we never detected clear ipsilateral responses in nucleus rotundus. Possibly the ipsilateral potential of the nucleus rotundus in normal birds is too small to be detected with our methods. Even with contralateral stimulation, the potentials recorded from nucleus rotundus are very small compared with the large ectostriatal responses. This may also reflect a different cellular organisation of the nucleus rotundus and the ectostriatum (Llinás and Nicholson 1974).

As yet it can not be excluded that the visual wulst of the thalamofugal pathway, in which ipsilateral stimulus processing is very common, is involved in the processing of ipsilateral stimuli in the tectofugal pathway, as projections from the visual wulst to the tectum opticum and ectostriatum have been demonstrated (Karten 1969; Karten et al. 1973; Ritchie and Cohen 1977; Nixdorf and Bischof 1982; Bagnoli and Burkhalter 1983; Watanabe et al. 1985). However, this seems to be unlikely, as the projections between the two systems have been described to be mainly inhibitory (Bagnoli et al. 1979). Moreover, we have indications that the latencies of the wulst responses are too long to be the source of the ipsilateral ectostriatal response (Bredenkötter et al. in prep.).

From an ethological point of view, two demands on the system connecting the two eyes can be formulated. Firstly, a mechanism should exist, which decides in a conflicting situation, for example the occurrence of a predator on the one side and food on the other, which stimulus has to be attended to. This stimulus should then be processed with priority and without disturbing effects from the other eye. Secondly, however, one has to propose that in no situation the eye contralateral to the actually processed important stimulus should be switched off totally, as it should be warranted that new stimuli on that side can be detected.

Our results demonstrate how such demands can be fulfilled by the tectofugal system. In normal situations, without heavy asymmetrical stimulation, the tectofugal system is balanced between the two eyes, each eye also occupying a certain area of the ipsilateral ectostriatum. If one eye is heavily stimulated, the ipsilateral influence of the other eye is switched off, whereas the ipsilateral influence of the stimulated eye persists. Therefore, the information from the stimulated eye is processed by the whole ectostriatum of the contralateral hemisphere and, in addition, part of the ipsilateral side. Processing of information from the other eye is not fully suppressed, but restricted to a part of the contralateral ectostriatum.

The recordings from unilaterally enucleated birds demonstrate that very small intensities of light or even the spontaneous ganglion cell activity of the unstimulated eye lead to a very prominent inhibition of the ipsilatral projection. Therefore, it is likely that the mechanism proposed above not only works in enucleated birds but also under natural conditions with only slight imbalances between the inputs of the two eyes.

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