8 The Organization of the Tectofugal Pathway in Birds: A Comparative Review

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In higher vertebrates visual information is processed by two prominent parallel pathways: the geniculocortical and extrageniculocortical pathways of mammals and the thalamofugal and tectofugal pathway in birds (e.g., Polyak, 1957 and see chapter 6; figure 8.1). The geniculocortical pathway includes the lateral geniculate nucleus (LGN) of the thalamus, area 17 (primary visual cortex, V1) of the striate cortex, and areas 18 and 19 in the extrastriate cortex. The extrageniculocortical pathway includes the superior colliculus (mesencephalon), the thalamic nucleus lateralis posterior (diencephalon), and telencephalic projection areas including the lateral suprasylvian cortex (reviews in Hubel and Wiesel, 1977; Creutzfeldt, 1988). Its avian counterpart, the tectofugal pathway, includes the optic tectum (mesencephalon), thalamic nucleus rotundus (diencephalon), and ectostriatum (telencephalon). The thalamofugal pathway (retino-lateral geniculate nucleus-Wulst) was reviewed in chapter 7. This chapter reviews the anatomy and physiology of the tectofugal pathway within a comparative perspective.

A substantial body of anatomical, physiological, and neurobehavioral (lesion) data, gathered over the past few decades, suggests that the dual sets of pathways in birds and mammals are homologous (Karten, 1969; Revzin and Karten, 1966; Revzin 1969, 1970, 1979; Kimberly et al., 1979; Miceli et al., 1979; Hodos et al., 1986; Wilson, 1980b; Denton, 1981; Shimizu and Karten, 1990). Perhaps, because that same period saw an explosion of research on the geniculostriate pathway (Hubel, 1982; Wiesel, 1982), studies in birds have focused primarily on the geniculocortical homologue: the thalamofugal pathway. The discovery by Pettigrew and Konishi (1976a,b) of some striking similarities between the visual Wulst of owls and mammalian visual cortex reinforced the thalamofugal focus.

However, owls, unlike most birds, have frontally placed eyes, resulting in significant overlap of the left and right hemifields and allowing binocular vision in a large region in front of the birds. In mammals like cats, monkeys, and man, binocular vision has been shown to allow precise distance estimation by neurons, which are sensitive to the dis-

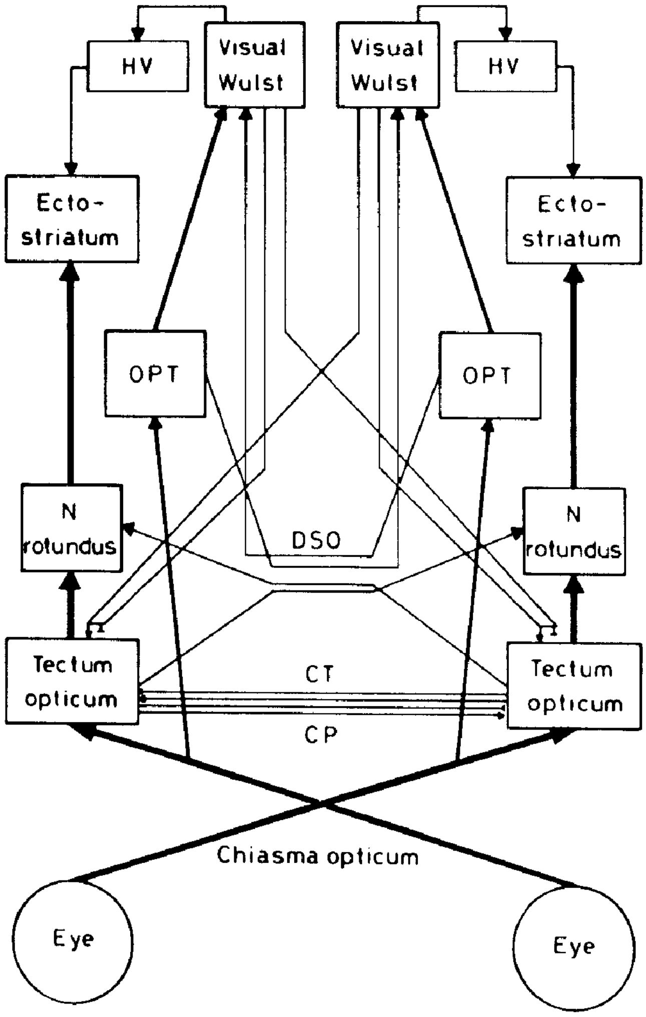


Figure 8.1 Main projections of the tectofugal and the thalamofugal pathway. Thick lines, tectofugal pathway; medium lines, thalamofugal pathway; thin lines, interhemispheric connections (DSO, CT, and CP) and connections between the two main pathways (HV → ectostriatum). DSO, decussatio supraoptica; CT, commissura tectalis; CP, commissura posterior; OPT, nucleus opticus principalis thalami; HV, hyperstriatum ventrale.

parity of the images on both eyes (e.g., Pettigrew, 1978), and has been presumed to facilitate detection of camouflaged objects. Both features would be especially useful for diurnal and nocturnal raptors. Thus, binocular vision in owls, and other diurnal raptors like falcons and kestrels, may be adaptive specializations to the demands of hunting prey. Several studies (Stingelin, 1958; Henke, 1983) have concluded that the relative size of the thalamofugal pathway and the degree of organization of the visual Wulst are related to the degree of binocular overlap, and this conclusion is supported by the comparative data of Pettigrew and his colleagues (Bravo and Pettigrew, 1981; Bravo and Inzunza, 1983).

Unlike owls, most birds have laterally placed eyes and a much less well-developed thalamofugal pathway. Indeed, it has long been evident that the tectofugal pathway is the most prominent pathway in birds

(Karten, 1969, Karten et al., 1973; Cohen and Karten, 1974). Moreover, the visual Wulst of lateral-eyed birds such as chicks, pigeons, and finches does not process ipsilateral or binocular visual information to a significant extent (Perisic et al., 1971; Wilson 1980b; Denton, 1981; Bredenkötter and Bischof, 1990). Neurobehavioral studies of the two pathways in pigeon—a lateral-eyed bird—indicate that tectofugal lesions produce severe discrimination deficits, while thalamofugal pathway lesions show obvious effects only if combined with lesions of the tectofugal pathway (Hodos et al., 1982; Watanabe et al., 1984, 1986). Finally, a rapidly growing body of data suggests that, in laterally eyed birds, the tectofugal pathway mediates some visual processes performed in mammals primarily by the geniculocortical pathway and by the thalamofugal pathway in frontal-eyed birds. Specifically, these data indicate that in laterally eyed birds simultaneous processing of visual information from both eyes and binocular interaction is carried out by the tectofugal visual pathway.

ANATOMICAL ORGANIZATION OF THE TECTOFUGAL VISUAL PROJECTIONS

In both birds and mammals, the optic nerves project in a highly ordered manner onto their primary visual target areas in the mesencephalon and diencephalon. The visual space of the external world is represented as an array of receptive fields on a map in the visual target areas in birds and mammals. The representation of visual information in a topographical order is probably maintained up to the primary sensory target areas of the telencephalon and in many cases even up to the secondary projection areas of the visual pathways.

In most mammals, the decussation of the optic nerve is only partial, the proportion of uncrossed fibers varying from as little as 10% in the rabbit to 50% in primates and man (Polyak, 1957). In contrast, the optic nerves of adult birds are virtually completely crossed (see, e.g., McLoon, 1982; McLoon and Lund, 1982; Bagnoli et al., 1987). The retinal projection on the contralateral tectum is probably retinotopically organized (Hamdi and Whitteridge, 1954). While there is no clear evidence for a topographic projection of the retinogeniculate (GLd) projection, it is known that in owls and falcons the temporal retina, representing the binocular visual field, projects heavily on GLd (Bravo and Pettigrew, 1981; Bravo and Inzunza, 1983). In contrast, the dorsotemporal retina (red field) of lateral-eyed birds projects almost exclusively on the optic tectum, while the much larger yellow field of the central retina projects on both tectum and GLd. Moreover, the retinal projection on GLd is generally much smaller than its projection on the tectum (Remy and Güntürkün, 1991). Even in more frontal-eyed birds, more than 60% of the retinal efferents terminate in the optic tectum (Bravo and Pettigrew, 1981).

The optic tectum is a highly laminated structure within which 6 (Cowan et al., 1961) to 15 (Cajal, 1891) layers may be distinguished. Retinal efferents form the superficial layers (mainly the stratum opticum) of the optic tectum. The projection is topographically organized. Tectal efferents arise from the deeper layers, mainly the stratum griseum centrale (SGC). The optic tectum is also the recipient of thalamofugal efferents from the visual Wulst (Bagnoli et al., 1980), providing a link between the two visual pathways. Electrophysiological studies indicated that the tectal projection on the thalamic nucleus rotundus projection may also be topographically organized (Revzin and Karten, 1966); and anatomical analysis reveals four or five subdivisions of rotundus, whose functional significance is not known (Benowitz and Karten, 1976; Nixdorf and Bischof, 1982; Bischof and Niemann, 1990; Martinez-de-la-Torre et al., 1990).

The nucleus rotundus projects ipsilaterally on the ectostriatum, a telencephalic structure divisible into "core" and "belt" regions, but little is known of the organization of the projection (Karten and Hodos, 1970; Benowitz and Karten, 1976; Nixdorf and Bischof, 1982). It is generally assumed that thalamic input reaches the "core" region, which then projects on the ectostriatal "belt," which may also receive Wulst efferents (Ritchie and Cohen, 1977; Watanabe et al., 1985). The subsequent intratelencephalic connections of the tectofugal pathway include a projection from ectostriatal "belt" to the neostriatum intermediale laterale (NIL), which, in turn, projects on the archistriatum intermedium (AI). AI projects on the optic tectum, completing a tectofugal loop made up of linked tectal–thalamic–telencephalic structures. Karten and Shimizu (1991) suggested that this nuclear circuitry resembles, in its general organizational pattern, the connectivity pattern of mammalian cortical layers (see chapter 6).

A "second" tectofugal pathway (Gamlin and Cohen, 1986) originates in the tectum, relays in the caudal dorsolateral posterior nucleus of the thalamus (DLPc), and terminates in specific areas of the intermediate and caudal neostriatum (NI, NC). The existence of still another telencephalic visual projection area was suggested by the finding of visual evoked potentials in the caudolateral telencephalon, with response latencies shorter than those recorded from Wulst and ectostriatum, but its input source has not been identified (Güntürkün, 1984).

RESPONSE PROPERTIES OF NEURONS IN THE TECTOFUGAL PATHWAY

Despite the relative paucity of physiological studies of the visual pathways in birds (see Granda and Maxwell, 1979), there are some data on the response properties of neurons at several levels of the tectofugal pathway. It has long been known, for example, that avian retinal ganglion cells can perform complex analyses of visual properties such as horizontal edge detection and direction selectivity (Maturana and Frenk, 1963). Early studies of tectal neurophysiology (e.g., Hamdi and Whitteridge, 1954) demonstrated a point-to-point representation of the pigeon's visual space on the optic tectum. The upper half of the left visual field is represented on the upper surface of the right optic tectum and the horizontal meridian is projected onto the lateral edge of the optic tectum. Within this projection, the spatial extension of the horizontal meridian is magnified in the tectal map. Bilge (1971) reported an increase in receptive field size from about 2°–3° in the superficial layers to up to 70° × 180° in the deeper layers (namely the SGC). A substantial proportion (ca. 70%) of tectal neurons is sensitive to moving stimuli and about 30% of these show a high degree of directional specificity, i.e., stimulation in the preferred direction of movement increases spontaneous firing rate, stimulation in the "null direction" leads to a reduction in firing rate (Jassik-Gerschenfeld and Guichard, 1972). However, most tectal units are only broadly tuned for direction and the majority prefer forward or downward directions of movement (Frost and DiFranco, 1976). Subsequent studies (Frost et al., 1981) have shown that tectal neurons are inhibited if the stimuli (e.g., white disks) and a structured background were moved in phase, but facilitated if the stimuli were moved in a direction opposite to the background. In addition to these properties, about 30% of tectal cells showed clear chromatic responses in their action spectra as well, i.e., they may be involved in color vision (Varela et al., 1983).

It appears that the responses of tectal neurons may be modulated by thalamofugal inputs relayed via visual Wulst efferents to the optic tectum (e.g., Bagnoli et al., 1982). Bagnoli et al. (1977, 1979) showed that both single unit activity and the prominent P wave of the tectal slow field potential (Holden, 1968) are reduced by concurrent activation of the optic tectum and the visual Wulst. This effect is time locked, i.e., the P wave completely disappears only if the visual Wulst is stimulated 30 msec prior to the optic tectum. Leresche et al. (1983) found that while the responses of most tectal cells to visual stimulation are clearly reduced during cooling of the visual Wulst, some direction-selective tectal units increase their responses. Thus visual Wulst input sharpens and facilitates neuronal responses in some cases and suppresses them in other cases. Neither the mechanism nor the functional significance of this observation is known.

The receptive fields of rotundal neurons are larger than those of tectal units but have similar characteristics, including preferential responses to moving stimuli with a clear directional, but no orientation, selectivity (Revzin, 1979; Maxwell and Granda, 1979). Revzin (1979) suggested a functional differentiation of the nucleus into a posterior third (responding to anything that moves, an anterior two-thirds (responding selectively to "abstract" stimulus characteristics such as size, direction, and velocity), and a ventral part, concerned primarily with brightness responses. Recently, Wang and Frost (1992) displayed computer-generated images of stimuli moving in spatial three-dimensional trajectories and found neurons in pigeon that apparently signal the time to collision with objects by simultaneously coding the speed and distance of a visual target. Finally, rotundal units also appear to have a selective response to the wavelength of light stimuli (Granda and Yazulla,, 1971; Maxwell and Granda, 1979). Opponent color units have been found in the nucleus rotundus of the pigeon (Yazulla and Granda, 1973) and in the nucleus geniculatus laterale pars ventrale (GLv), another thalamic nucleus receiving direct tectal input (Varela et al., 1983).

The few published studies of ectostriatal units have found (1) that most units were responsive to visual stimuli, (2) that they all had very large receptive fields, and (3) that the proportion of directionally selective cells is increased by comparison with retina, tectum, and rotundus. Most units prefer upward/downward or fore/aft movements, but none was selectively responsive to orientation (Revzin, 1970; Kimberly et al., 1971). Revzin (1979) suggested that the functional organization of the nucleus rotundus is simply relayed to the ectostriatal core. However, from the single unit data available, neither the existence nor nature of that organization is clear.

Using the methods of current source-density (CSD) analysis (e.g., Nicholson and Freeman 1975; for review see: Mitzdorf, 1985), Engelage and Bischof (1989) recorded contralateral and ipsilateral flash-evoked slow field potentials in the ectostriatum of the zebra finch. They found that the time course of macroscopic current sinks, indicating sites of excitatory synaptic activity; the negative wave of visual evoked potentials and single unit responses to the same stimulus match exactly (Figure 8.2). The most characteristic feature of the current source density depth profiles is an early prominent current sink (8.3:a) in the ectostriatal core, with corresponding dorsal and ventral current sources. A delayed sink (8.3:b)–source–sink (8.3:c) sequence located within the core region is also detectable in contralateral and ipsilateral CSD depth profiles. This clearly shows that the generators for the contralateral and ipsilaterally evoked visual potentials are located within the ectostriatal core (figure 8.3). Contralaterally and ipsilaterally evoked responses commonly show the same basic pattern of alternating sinks and sources in their CSD depth profiles (Engelage and Bischof, 1989). Macroscopic sinks and sources as shown above emerge only if during activation of the system neuronal assemblies become active concomitantly. The data therefore suggest that despite its homogeneous anatomical organization, the ectostriatum may have a high degree of physiological parcellation, reflecting the existence of distinct functional subdivisions.

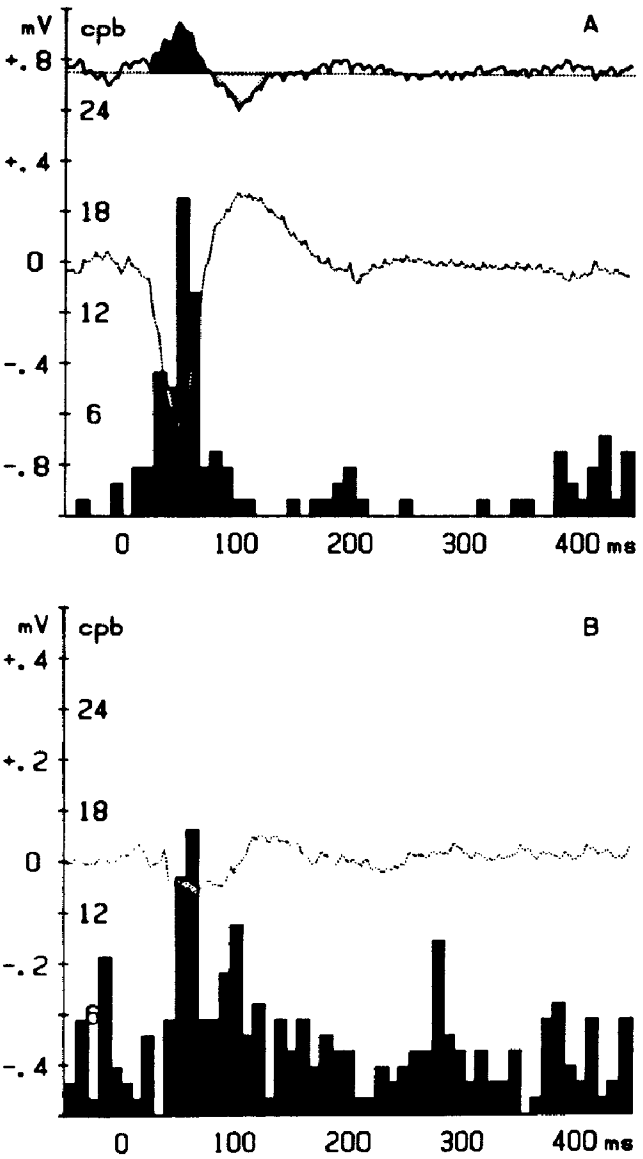


Figure 8.2 Flash-evoked slow field potential (VEP), current source-density profile (CSD), and single unit activity at an identical recording site in the ectostriatum of the zebra finch. (A) Contralateral stimulation; (B) ipsilateral stimulation. The stimulus is delivered at 0 msec. For the VEP response bin width is 500 μsec, average 64 ×, and the ordinate scale is in mV. Signals are filtered only by a 4-Hz highpass filter. CSDs are calculated according to the formula developed by Nicholson and Freemann (1975). As the differentiation grid for ectostriatal VEPs is 500 μm, the VEP traces 250 μm above and below the recording site had to be taken into account for the calculation of the CSD profile. For the single unit response bin width is 10 msec, average 16 ×, and the ordinate scale is in spikes/bin. Signals are band pass filtered with limits at 300 Hz and 10 kHz. The most important result of this comparison is the perfect agreement in the time patterns of VEP, CSD, and single unit activity. This shows that the three methods demonstrated reflect, to a high degree, the same physiological processes in ectostriatal visual processing.

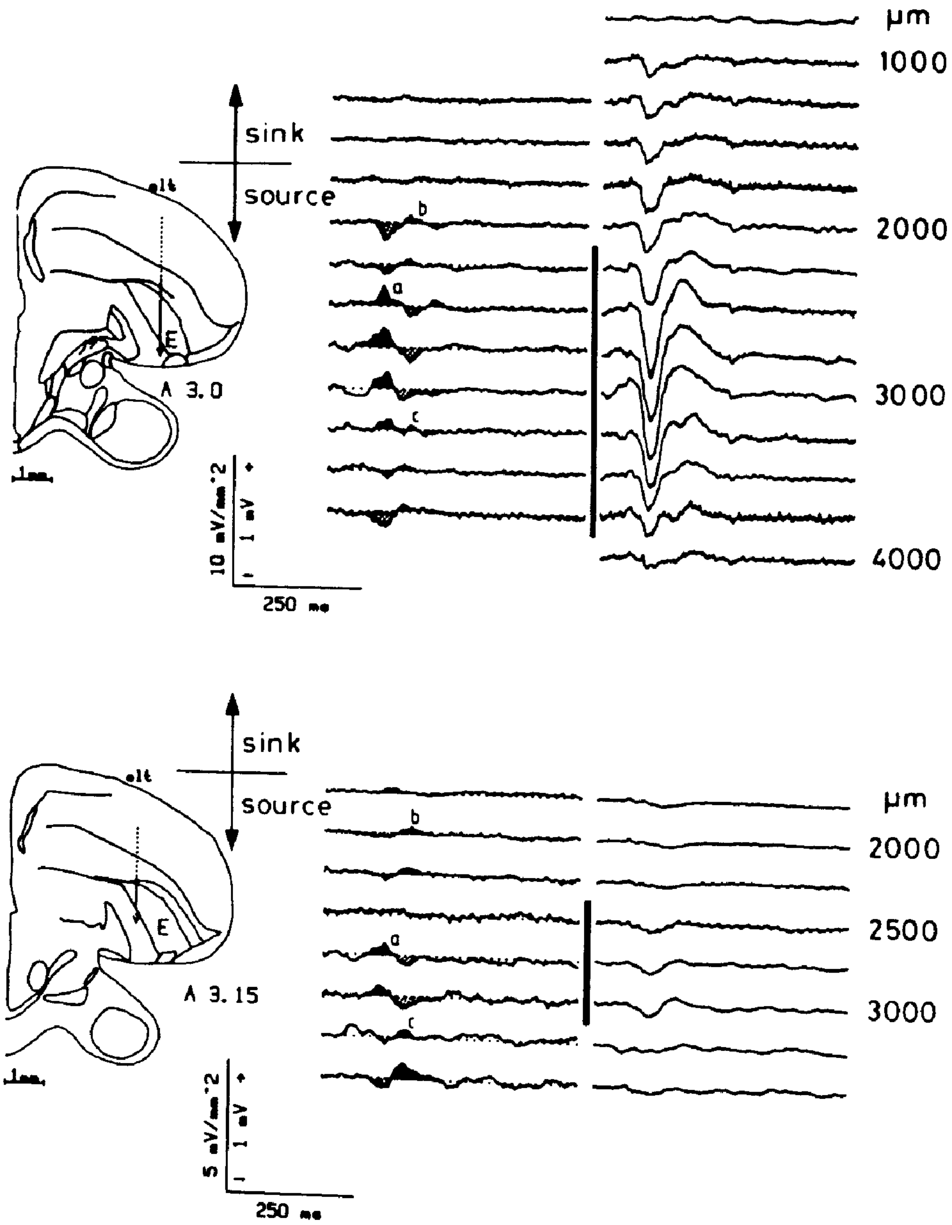


Figure 8.3 Comparison of contralateral (top) and ipsilateral (bottom) evoked potentials and related current source-density depth profiles in the ectostriatum of the zebra finch. (Left) Frontal sections (anterior 3.0 and 3.15) of the zebra finch brain with electrode tracks. (Middle) Current source-density depth profiles calculated from the VEP traces in the right column. Average 64 ×, bin width 500 µsec, step width 250 µm stimulus at 0 msec, differentiation grid for CSDs is 500 µm. Signals are filtered only by a 4 Hz highpass filter. CSDs are calculated according to the formula developed by Nicholson and Freemann (1975). The heavy bars represent the solid part of the electrode track markings in the left column. The figure clearly demonstrates that the generators for the contralateral and ipsilateral extracellularly recorded VEPS are located within the ectostriatal core region.

HEMISPHERIC INTEGRATION IN THE TECTOFUGAL PATHWAY

Because the optic chiasm is completely crossed in birds, both visual pathways in each hemisphere receive their primary visual information exclusively from the contralateral eye. Hence ipsilateral and binocular stimulus processing can be achieved only by secondary recrossing fibers connecting the visual target areas of the left and right hemispheres. Such fibers exist at several brain levels (see figure 8.1) and include the mesencephalic tectal commissure (CT) (Robert and Cuenod, 1969a) and the dorsal and ventral supraoptic decussations of the forebrain (DSOD, DSOV). In the thalamofugal pathway, recrossing fibers in DSOD connect the GLd complex to the visual Wulst of both hemispheres (Karten et al., 1973; Bagnoli and Burkhalter, 1982; Mihailovic et al., 1974). In the tectofugal pathway, recrossing fibers of the tectorotundal projection, traveling in DSOV, connect the optic tectum to the nucleus rotundus of the contralateral side (Benowitz and Karten, 1976) and have recently been shown to make a significant contribution (about 23%) to the efferent projections of the optic tectum (Bischof and Niemann, 1990).

For the thalamofugal pathway, the only known source for hemispheric interactions is the recrossing bilateral GLd–visual Wulst projection (Karten et al., 1973; Bagnoli et al., 1982). In lateral-eyed birds—e.g., zebra finches, pigeons, and chicks—the visual Wulst, though clearly responsive to contralaterally presented stimuli, is essentially unresponsive to ipsilateral or binocular stimuli (Parker and Delius, 1972; Denton, 1981; Wilson, 1980b; Bredenkötter and Bischof, 1990). For the tectofugal pathway, in contrast, multiple potential sources of hemispheric interaction have been demonstrated. At caudal levels, an inhibitory role for the tectal commissure is suggested by the report that about 25% of tectal neurons driven via the CT were inhibited during electrical stimulation of the contralateral optic tectum (Robert and Cuenod, 1969b), a finding later confirmed by intracellular studies in pigeon (Hardy et al., 1984, 1985) and evoked potential analyses in the zebra finch (Engelage and Bischof, 1988).

The early studies of thalamic and telencephalic tectofugal structures provided no evidence with respect to the processing of ipsilateral and bilateral stimuli (e.g., Revzin, 1966; 1970; Maxwell and Granda, 1979; Kimberly et al., 1971; Parker and Delius, 1972). However, Engelage and Bischof argued that the capacity for panoramic vision, seen in all lateral-eyed birds, must imply central access to ipsilateral (and binocular) visual inputs. Using visual evoked potential (VEP) methods, these investigators systematically examined thalamofugal and tectofugal structures in the visual system of the zebra finch, a lateral-eyed bird with only a small binocular visual field (Bischof, 1988). Their studies showed that, in contrast with the Wulst (Bredenkötter and Bischof, 1990), the ectostriatum is clearly responsive to contralaterally *and* ipsilaterally presented flashed stimuli (figure 8.4). The ipsilaterally evoked potentials reached

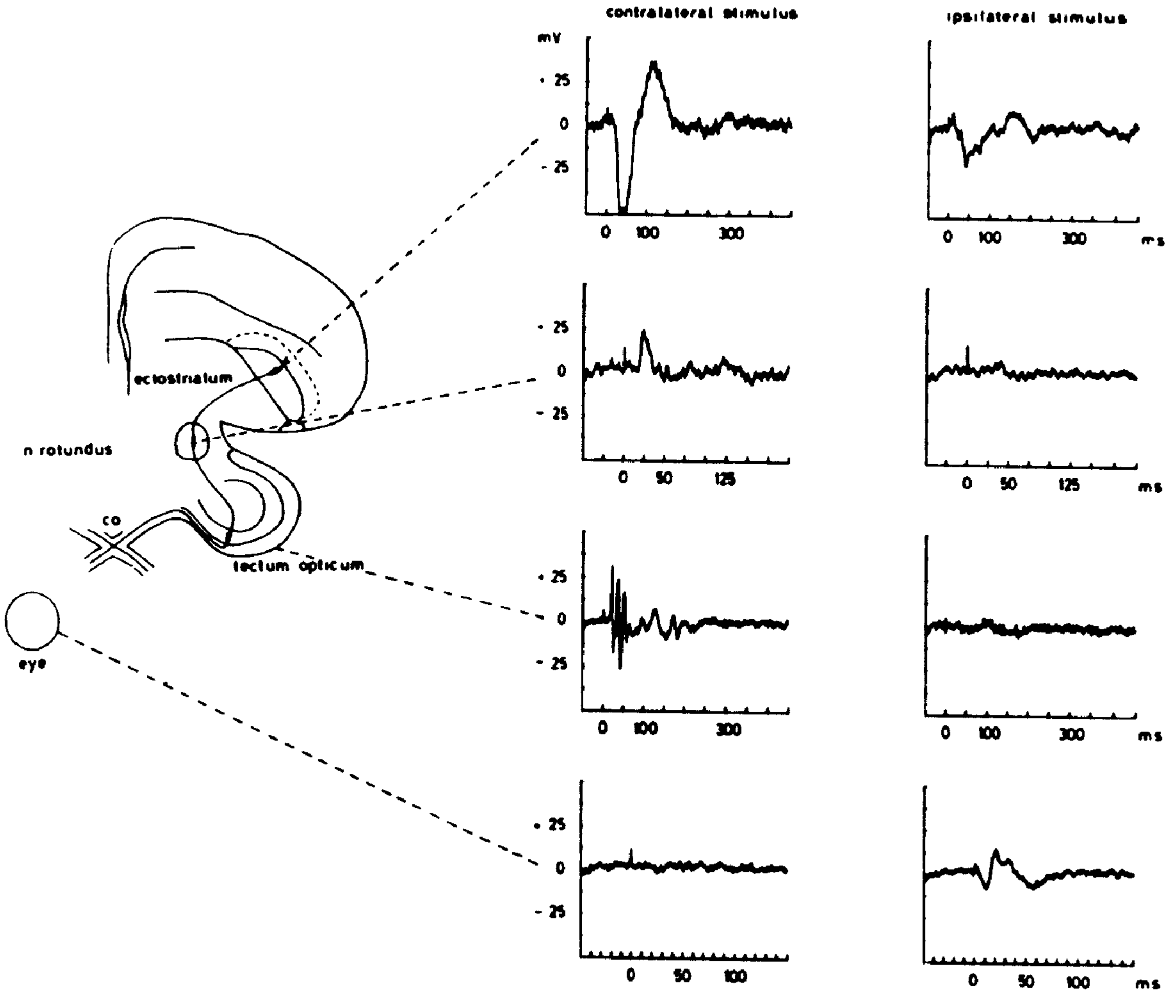


Figure 8.4 Averaged VEPs from the tectofugal pathway of the zebra finch. (Left) Simplified diagram (compare figure 8.1) of the pathway. (Right) Diagrams from bottom to top: recordings from eye, optic tectum nucleus, rotundus, and ectostriatum. (Left column) Contralateral stimulation. (Right column) Ipsilateral stimulation. Average 64 ×, bin width 200–500 μsec (see variations of the time scale), stimulus at 0 msec. Signals are filtered only by a 4 Hz highpass filter. The figure clearly shows that the ectostriatum receives information from the ipsilateral eye.

amplitudes up to 50% of contralaterally evoked responses (Engelage and Bischof, 1988).

Supporting evidence for tectofugal ipsilateral processing comes from some unexpected results of VEP recordings in unilaterally enucleated subjects. Ipsilaterally evoked ectostriatal VEPs in these birds were dramatically enhanced, with their highest amplitudes comparable to those of contralaterally evoked VEPs in normal zebra finches (figure 8.5). In contrast with the significant differences in amplitudes and latencies reported for normal birds, there were no significant differences in either parameter between ipsilaterally evoked VEPs in enucleated birds and contralaterally evoked VEPs in normal birds (Engelage and Bischof, 1988). Interestingly, ipsilaterally evoked VEPs could also be detected in the nucleus rotundus of enucleated but not of normal birds, but no

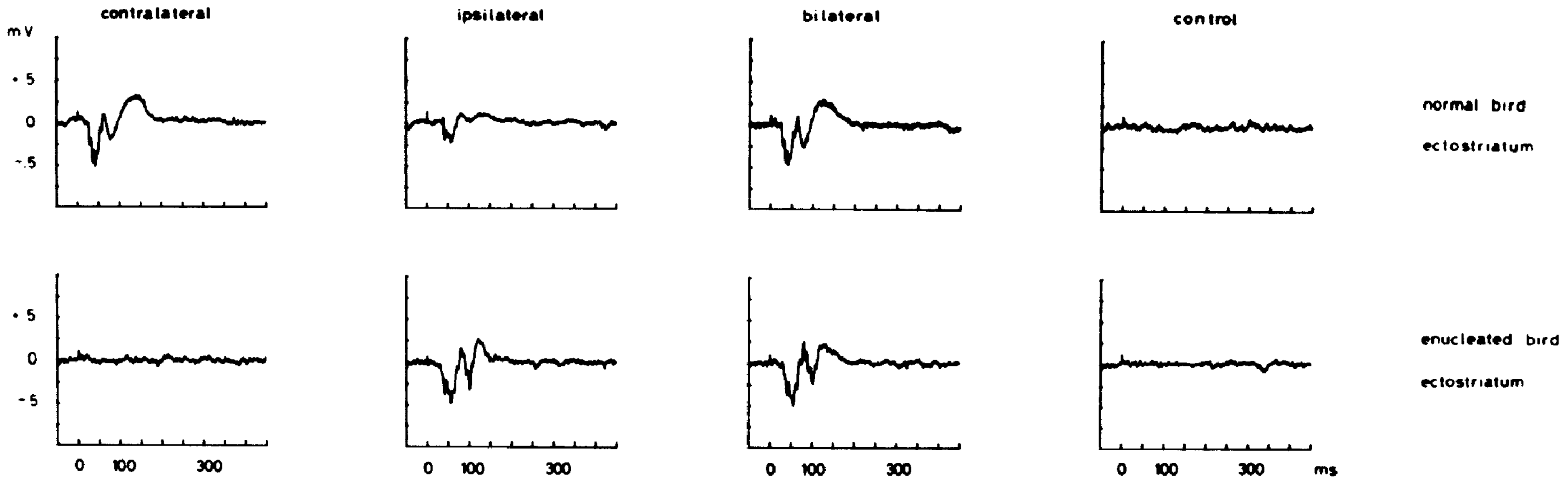


Figure 8.5 Summary of the effects of enucleation on responses of the ectostriatum in a bird enucleated 3 days prior to the recordings. In normal birds (upper row) contralateral and bilateral stimulus responses are very similar. Ipsilateral VEPs are about 50% smaller than contralaterally and bilaterally evoked VEPs. In enucleated birds (lower row) the situation is clearly changed. Ipsilateral VEPs reach amplitudes similar to contralateral VEPs in normal birds and are as high as bilaterally evoked VEPs. This clearly shows that ipsilateral stimulus responses are not due to light spreading from one eye to the other. As ipsilaterally evoked VEPs in enucleated birds are clearly enhanced, it is concluded that ipsilateral stimulus responses in normal birds are severely inhibited. Average 64 ×, bin width 500 μsec, stimulus at 0 msec. Signals are filtered only by a 4 Hz highpass filter.

ipsilateral VEPs were detected in the optic tectum. Experiments in the thalamofugal and tectofugal pathway compared the effects of an acute unilateral injection of tetrodotoxin (a substance blocking EPSPs) into the eye while recording from ipsilateral visual Wulst and ipsilateral ectostriatum. The facilitatory effects on VEPs seen in ectostriatum were not seen in the visual Wulst. Engelage and Bischof (1988) concluded that visual information is conveyed from the ipsilateral eye to the contralateral optic tectum, recrosses to the ipsilateral nucleus rotundus, and is finally conveyed to the ipsilateral ectostriatum, a conclusion consistent with the connectivity pattern of these structures (Karten et al., 1973; Benowitz and Karten, 1976; Hunt and Künzle, 1976; Nixdorf and Bischof, 1982; Bischof and Niemann, 1990).

These findings are also consistent with a major role for inhibitory mechanisms in ipsilateral stimulus processing in the ectostriatum. From a comparison of VEPs in different target areas in enucleated birds, Engelage and Bischof (1988) concluded that the spontaneous activity of retinal ganglion cells severely suppresses responsiveness in the ipsilateral ectostriatum of normal birds. This inhibition is probably generated by tectal crosstalk via the tectal commissure and intrinsic tectal circuits.

This "mutual inhibition" hypothesis was supported by experiments in which inhibitory synapses in the optic tectum were blocked by the application of picrotoxin. When applied to the optic tectum ipsilateral to the recording site in the ectostriatum, ipsilaterally and contralaterally evoked responses were substantially enhanced, but the enhancement was greatest for the ipsilateral responses. This shows that ipsilateral information must, to some extent, be conveyed from one optic tectum to the other. Picrotoxin injection into the optic tectum contralateral to the ectostrial recording site enhanced ipsilaterally, but not contralaterally evoked responses, demonstrating that ipsilateral stimulus responses are selectively inhibited in the optic tectum contralateral to the recording site (figure 8.6). The results are in agreement with those of the enucleation experiments.

Finally, experiments in which the neuronal activity of either the visual Wulst or the optic tectum was suppressed by either cooling or "spreading depression" (Leao, 1944) showed that the ipsilateral evoked responses observed in the ectostriatum are not primarily mediated by inputs relayed through the visual Wulst to the tectofugal ectostriatum. Ipsilaterally evoked ectostriatal potentials were significantly reduced but not abolished during suppression of ipsilateral Wulst activity. In contrast suppression of optic tectum activity ipsilateral to the ectostriatal recording site led to a decrease in ipsilateral responses and a severe reduction of contralateral responses. These experiments, while confirming an important role for tectal inhibitory processes, also suggest that the visual Wulst may have a significant excitatory influence on the processing of contralaterally evoked visual information in the ectostriatum (figure 8.7). Thus it cannot be excluded that both the recrossing

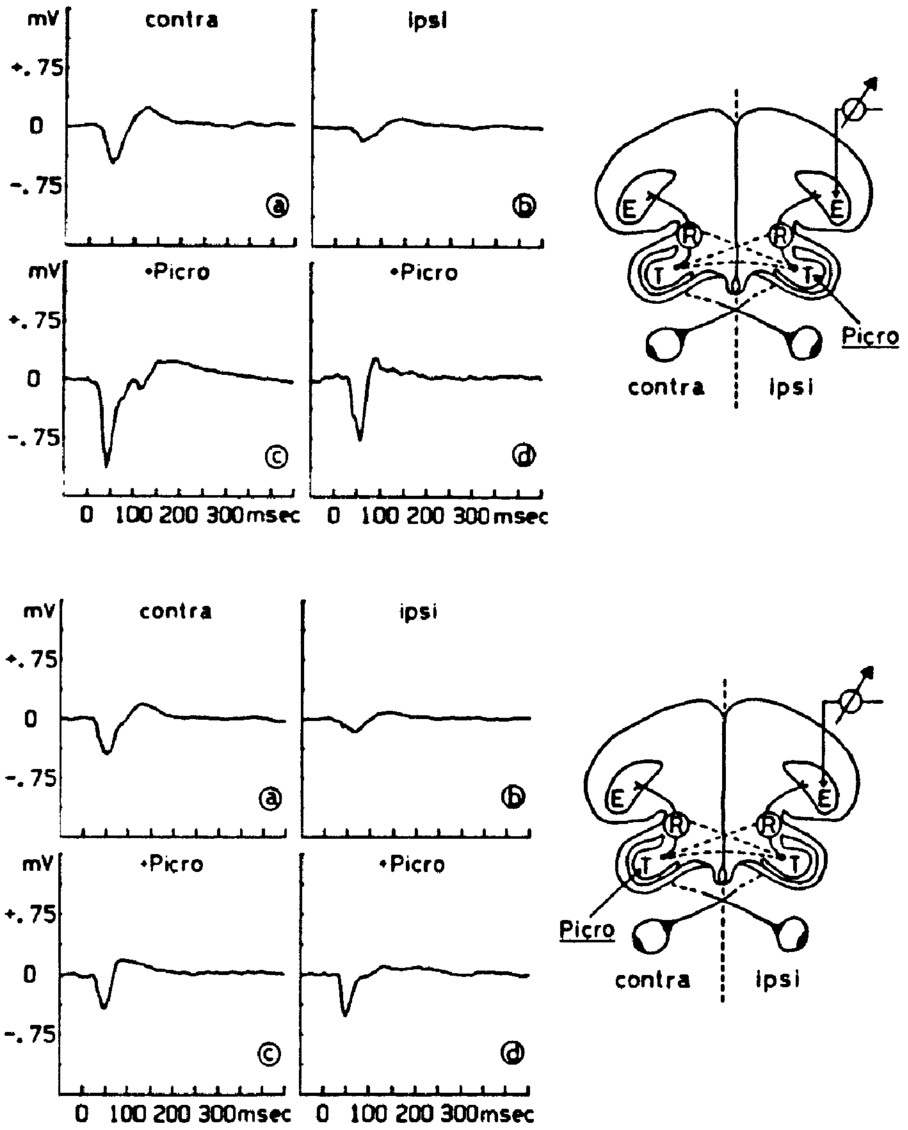


Figure 8.6 Changes in ectostriatal VEP responses during picrotoxin-induced disinhibition of the optic tectum contralateral and ipsilateral to the recording site in the ectostriatum. (Upper panel, a and b) Responses to contralateral and ipsilateral stimulation before picrotoxin injection; (c and d) responses after picrotoxin injection into the optic tectum ipsilateral to the recording site. (Lower panel, a and b) Responses to contralateral and ipsilateral stimulation before picrotoxin injection; (c and d) responses after picrotoxin injection into the optic tectum contralateral to the recording site. Injection into the ipsilateral optic tectum enhances ipsilateral and contralateral responses; injections into the contralateral optic tectum selectively enhances ipsilateral responses. Average 64 ×, bin width 500 μsec, stimulus at 0 msec. Signals are filtered only by a 4 Hz highpass filter. The results show the major importance of the tectal circuitry for the selective suppression of ipsilateral stimulus responses. The observed changes are also in perfect agreement with the results from the enucleation experiments reported above.

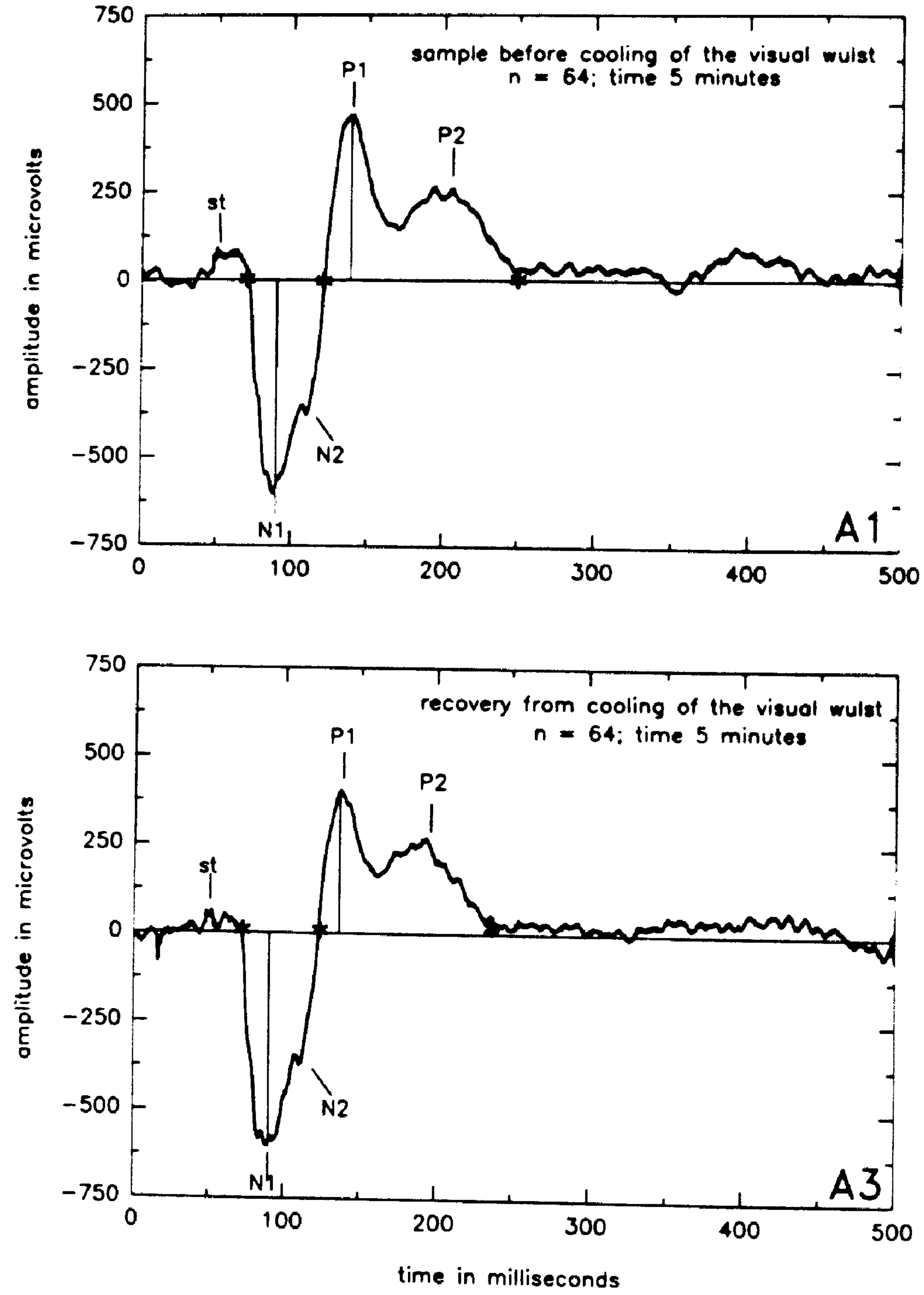
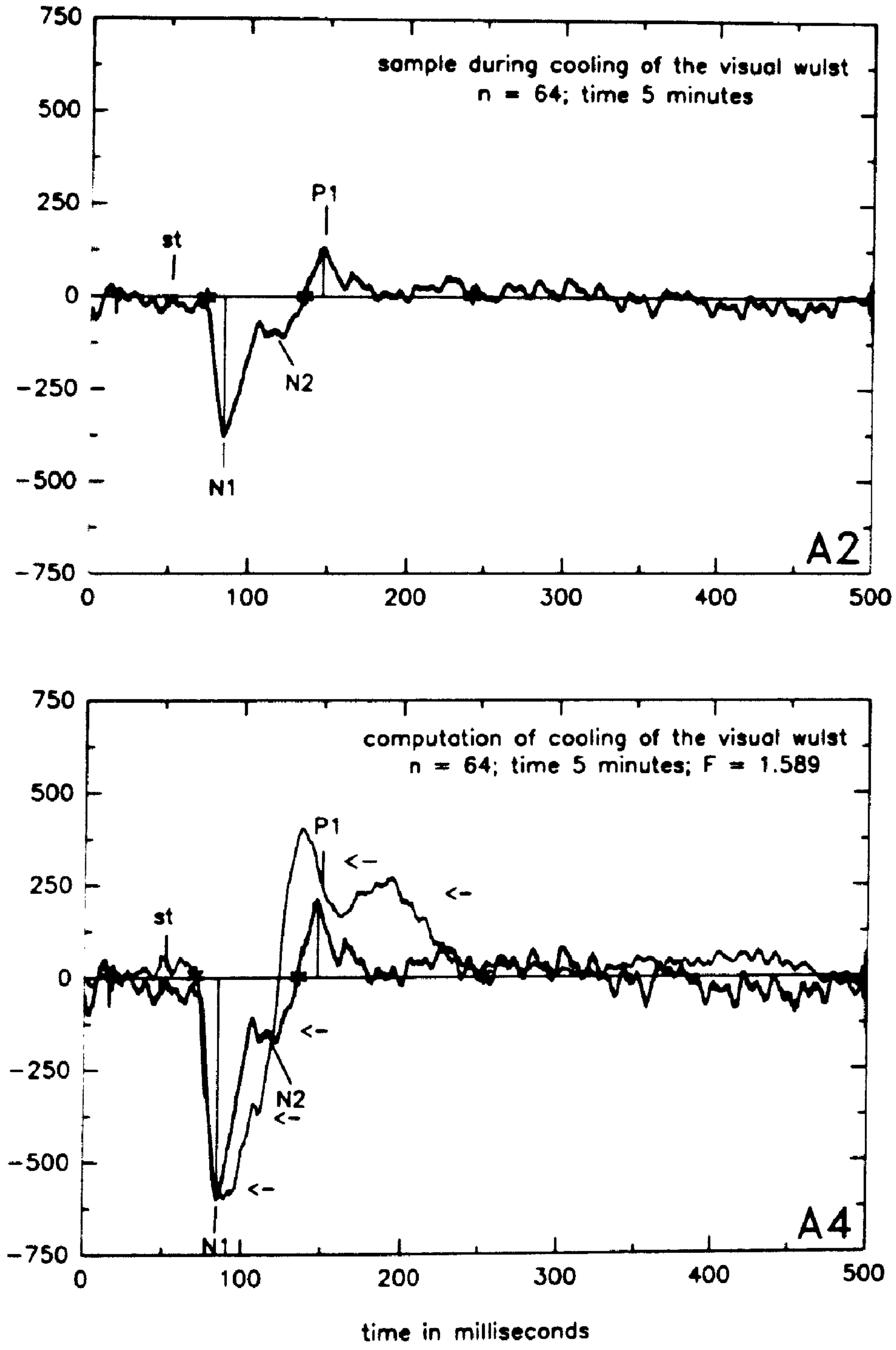


Figure 8.7 Changes in contralateral ectostriatal VEPs during cooling of the visual Wulst ipsilateral to the recording site. (A1) before cooling; (A2) during cooling; (A3) recovery from cooling; (A4) computer simulated amplitude enhancement of VEP wave. Amplitude enhancement was achieved by multiplication of each bin with the quotient from maximal amplitude of the negative wave from recovery divided by maximal amplitude of the negative wave during cooling. Superimposed (thin line) is the VEP recorded after recovery (A3). The arrows indicate the major differences between the VEPs recorded during and



after cooling of the visual Wulst. Thin horizontal lines mark the zero line and thin vertical lines mark the locations of amplitude measurements. Average 64 ×, bin width 500 µsec, stimulus at 50 msec. Signals are filtered only by a 4 Hz highpass filter. Note the severe amplitude reduction of N1 and P1 and the almost complete diminution of N2 and P2 due to the suppression of visual Wulst activity indicating an excitatory contribution of visual Wulst efferents to ectostriatal visual stimulus processing.

optic tectum, nucleus rotundus projections, and the visual Wulst, optic tectum projections, make some contribution to the marked inhibition of ipsilateral stimulus responses.

NEUROBEHAVIORAL STUDIES OF THE TECTOFUGAL PATHWAY

In contrast to the minimal effects of the thalamofugal pathway lesions, it has been repeatedly found that damage restricted to one or more tectofugal structures produced significant deficits on a variety of visually guided tasks, including color, brightness, pattern, and size discriminations. Particularly in spatial resolution tasks, combined thalamotectofugal pathway lesions produce significantly more severe deficits than lesions restricted to the tectofugal pathway alone (Macko and Hodos, 1984; Hodos et al., 1984). The finding of deficits in line orientation after rotundal lesions (Mulvanny, 1979) suggests the existence of orientation-selective units in the tectofugal pathway despite the absence of supporting electrophysiological evidence. Moreover, the tectofugal, rather than the thalamofugal pathway is critical for the mediation of interocular transfer of visual discrimination learning (Watanabe et al., 1986; Remy and Watanabe, this volume). Finally. Hodos et al. (1982) showed that following rotundal lesions (which normally produce substantial brightness discrimination deficits), a second lesion in the ventrolateral geniculate nucleus (a tectofugal fiber recipient) virtually diminished the deficits produced by the first lesion. These investigators discussed their findings in the context of parallel processing of visual information and a modulatory contribution of the different visual target areas to information processing.

The contribution of the second tectofugal pathway remains unclear. Single unit recordings (Korzeniewska and Güntürkün 1990) showed that its nuclear component (DLP) is multimodal, responding to both somatosensory and visual inputs. Lesion studies (Hodos et al., 1986; Kertzmann and Hodos, 1988) revealed the same pattern as observed in the thalamotectofugal comparisons. Only if combined with lesions in the "first" tectofugal pathway, lesions in thalamic and telencephalic targets of the "second" tectofugal pathway led to significant deficits in visual discrimination tasks.

Taken together, the results of all these studies are consistent with (1) a dominant role for the tectofugal pathway in visual discriminations of colors, brightness, and patterns, (2) a supportive role for thalamofugal structures in mediating spatial resolution, and (3) the importance of interaction between the two major visual pathways. The tectofugal pathway, acting in isolation, appears capable of mediating a substantial part of the visual processing carried out by birds. A similar view is gradually coming to be held with respect to the homologous visual pathways in mammals (Creutzfeldt, 1988).

CONCLUSIONS

The functional contribution of the tectofugal pathway to the processing of visual information is far from clear. The optic tectum receives a point-to-point projection from the retina, and the receptive fields of the outer tectal layers are small enough to allow for a precise localization of objects within visual space. However, because the subsequent targets of tectal projections to diencephalic and telencephalic structures have large receptive fields (as well as the inner tectal layers), these structures may be more concerned with the analysis of directionality, orientation, and velocity of moving objects, and the processing of colors, contours, and other more general features of the visual scene. Paradoxically, however, lesion studies indicate that despite their large receptive fields, higher levels of the tectofugal pathway may also be involved in the analysis of fine visual detail. This could be achieved by small subunits within the large receptive fields or by additional modulatory inputs from the thalamofugal pathway. Whatever the mechanism, the tectofugal pathway is probably involved in almost all types of visual information processing. Even the processing of binocular information, which until recently was thought to be an exclusive domain of the thalamofugal pathway, is, in lateral-eyed birds, performed mainly by the tectofugal pathway.

A persistent problem for investigators concerns the functional significance of the physiologically and morphologically defined subdivisions of rotundus. It is not known whether these subdivisions comprise independent topographical maps or not and how they project to the ectostriatum. More information is needed on the intrinsic organization and neostriatal projections of ectostriatum, and the role of the Wulst projection on its "belt" region. A second problem is raised by the existence of an anatomically defined tectothalamic–telencephalic–tectal feedback loop. One of its possible functions may be the modulation of incoming information flow by descending telencephalic inputs. Another would be the comparison, at tectal levels, of incoming visual information with inputs from higher centers, its integration with other tectal sensory inputs, and its projection on final common path behavioral mechanisms. Finally, given the emerging picture of a dominant tectofugal pathway, and a pattern of information flow from thalamofugal to tectofugal structures, but not vice versa, what role is left for the thalamofugal pathway in lateral-eyed birds?

Investigations with 2-deoxyglucose suggest that the visual Wulst is active only in awake, aroused birds, while the ectostriatum shows a high level of spontanous activity under almost all conditions (Bischof and Herrmann, 1986). The functional implications of this observation are presently obscure. Moreover, because both pathways are likely to be involved simultaneously in almost any task, e.g., binocular processing, the determination of their separate functions in isolation is likely to be both empirically difficult and conceptually erroneous. Finally, the function of different parts of the visual system appears to have changed during evolution. Despite such difficulties, this review testifies to the progress that has been made in clarifying the role of tectofugal structures in visual processing by birds.

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