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Development of flash-evoked responses in the ectostriatum of the zebra finch: An evoked potential and current-source-density analysis

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Abstract

The morphological development of the tectofugal pathway in the zebra finch has recently been described in a series of studies from our laboratory. No data are currently available on the development of visual responsiveness in this pathway. We therefore investigated the development of visually evoked potentials (VEPs) in the ectostriatum, the telencephalic target area of the tectofugal pathway. Contralateral VEPs could already be recorded in 20-day-old birds, whereas ipsilateral VEPs could first be recorded in 40-day-old birds. The latencies of contralateral VEPs decrease to adult values between 20 and 40 days of age, probably due to an increase in the myelination of afferent fibers. The amplitudes of the contralateral VEPs increase continuously from day 20 to day 60; however, between 60 and 80 days of age the responses diminish substantially (−60%). Thus, contralateral VEPs in 80-day-old birds are not significantly different from those in 20-day-old birds. Thereafter the responses recover and reach their final amplitude values at about 150 days of age. The relationship of these results to morphological studies and possible mechanisms which may cause the double-peaked development of visual-evoked potentials in the ectostriatum are discussed.

Keywords: Zebra finch, Development, Ectostriatum, Visual-evoked potentials, Current source density

Introduction

In contrast to rather detailed studies in mammals, information on the function and development of visual structures in birds is very limited. Information about function and development of visual processing in the thalamofugal pathway is only available from a highly specialized nocturnal bird, the barn owl (*Tyto alba*), (Pettigrew & Konishi, 1976*a*,*b*). In the avian tectofugal pathway, which is presumably homologous to the extrageniculate pathway of mammals, recent studies from our laboratory demonstrate that developmental processes can be influenced by environmental manipulations similar to those used in studies of the mammalian geniculocortical pathway (Herrmann & Bischof, 1986*a*,*b*,*c*; Herrmann & Bischof, 1988*a*,*b*; Nixdorf & Bischof, 1986, 1987). Two main conclusions can be drawn from these data. Firstly, the morphological development of the tectofugal system is obviously complete by day 40 coinciding with the end of the sensitive phase for monocular deprivation (Herrmann & Bischof, 1988*a*). Secondly, the major effects of monocular deprivation are localized in the hemisphere driven by the non-deprived eye (Herrmann & Bischof, 1986*a*,*b*,*c*; Herrmann & Bischof, 1988*a*,*b*; Nixdorf & Bischof, 1987). As no direct ipsilateral retinal projection exists in the visual system of birds (as is the case in mammals), this implies the existence of interhemispheric connections in the tectofugal system of birds. These hemispheric interactions seem to partially protect the non-deprived hemisphere from the regressive events that normally occur during development of the tectofugal system such as a massive reduction of dendritic spines (Herrmann & Bischof, 1986*a*,*b*,*c*; Herrmann & Bischof, 1988*a*,*b*). Electrophysiological studies have indeed demonstrated massive processing of ipsilateral stimuli in the tectofugal visual pathway of birds (Engelage & Bischof, 1988, 1989). No electrophysiological data on the development and plasticity of the avian tectofugal pathway are available. Such data will be valuable for the interpretation of anatomical findings and for a comparative analysis of developmental processes in birds and mammals.

We therefore investigated the normal development of the physiological response properties of the ectostriatum, the telencephalic target area of the tectofugal pathway of birds with recordings of ectostriatal visual-evoked potentials (VEPs), and a current-source-density (CSD) analysis in birds of different ages.

Materials and methods

Data was collected from 15 juvenile zebra finches of both sexes. Recordings were made in three birds at 20, 40, 60, 80, and 100

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days of age, respectively. The results were compared with previous data from 15 adult zebra finches (Engelage & Bischof, 1988, 1989).

Preparation, stimulation, and evoked-potential recording

The birds were deeply anesthetized with an intramuscular injection of 0.1 ml urethane (20% w/v) and mounted on a stereotaxic headholder (Bischof, 1981). Evoked potentials were recorded with glass micropipettes filled with alcian blue in 3 M NaCl (5–15 MΩ). The indifferent electrode was placed in the neck muscles of the bird. Coordinates for the electrode positions were derived from an atlas of the zebra finch brain (Bischof & Nixdorf, unpublished data).

All electrode tracks presented below and included in the analysis were recorded at the same stereotaxic coordinate (anterior 3.15 mm and lateral 3.5 mm) as there is some variation between VEPs from different ectostriatal areas (Engelage & Bischof, 1988, 1989). This method appears adequate as anatomical data demonstrate no difference in brain size between 20-day-old birds and adult birds. Moreover, in several animals of all age groups we recorded VEPs from different areas in the entire ectostriatum.

Visual stimuli were provided by a stroboscope. Flashes of 0.5-ms duration were directed to one or both eyes by a fiber optic system. The stimulus distance was less than one centimeter and therefore served as a "Ganzfeld" stimulus. Contralateral, ipsilateral and bilateral stimuli were selected by opening and closing shutters between the stroboscope and the fiber-optic system. The terms ipsilateral and contralateral refer to the position of the recording electrode in reference to the stimulated eye. Control data was obtained by closing both shutters or by removing the fiber-optic system from the eyes.

Signals were averaged 64 times by a Nicolet signal averager. The interstimulus time interval was 5 s. Signals were only filtered by a 12-Hz high pass filter. Storing and processing of the data was accomplished by a HP-86 microcomputer. This device also triggered the stimuli and controlled the experimental procedure. Maximum amplitudes and peak latencies were estimated by microcomputer. Detailed information on amplitudes and latencies was obtained by processing the evoked-potential plots on a graphics tablet.

CSD analysis

The extracellular field potential Φ is related to the active and passive transmembrane currents of cell assemblies of activated neurons by the Poisson equation:

$$\vec{\nabla} \times \sigma \times \vec{\nabla}\phi = -I_m. \tag{1}$$

Assuming a homogenous structure and translational symmetry in two dimensions, the current sinks and sources are proportional to the second spatial derivative of the extracellular VEPs in the direction of the respective electrode track [eq. (2), e.g. Mitzdorf, 1985; Nicholson & Freeman, 1975].

$$-I_m(z,t) = \sigma(z,t) \times \frac{\delta^2\phi(z,t)}{\delta z^2}, \tag{2}$$

where

I_m = volume current sink and source density,
σ = conductivity tensor of the extracellular space,
z = axis of the electrode penetration,
t = time,
Φ = extracellular field potential.

The second spatial derivatives of the VEPs have been approximated by numerical differentiation (Mitzdorf & Singer, 1977, 1978) with the finite-difference formula according to Mitzdorf and Singer (1977):

$$-I_m = \frac{\delta^2\phi(z)}{\delta z^2} \approx \frac{\phi(z + n \times \Delta z) - 2\phi(z) + \phi(z - n \times \Delta z)}{(n \times \Delta z)^2}, \tag{3}$$

where

I_m = volume current sink and source density,
σ = conductivity tensor of the extracellular space,
z = axis of the electrode penetration,
Δz = distance of successive measurements,
$nx\Delta z$ = differentiation grid,
Φ = extracellular field potential.

We used step widths (Δz) of 50–250 μm and differentiation grids ($nx\Delta z$) in the range 200–500 μm. The optimal differentiation grid for each profile was determined empirically (e.g. Mitzdorf, 1985). Applying the current-source-density analysis in its simple one-dimensional form implies constant conductivity and translational invariance in the nervous tissue from which recordings have been made (e.g. Mitzdorf, 1985; Nicholson & Freeman, 1975). The validity of these assumptions in the ectostriatum has been discussed elsewhere in more detail (Engelage & Bischof, 1989).

Statistics

The significance of the differences in the amplitude and latency distribution between the different age groups was tested by multiple two-tailed Student's t-tests and Mann–Whitney U tests (Sinclair, 1988). In comparing both amplitudes and latencies, we used a sample of 21 values of each different age, these consisted of seven values from different recording depths at the standard stereotaxic coordinates in the ectostriatal core region in each of three birds.

Results

Adult birds

Contralateral stimulus responses in the ectostriatum of adult zebra finches (see Fig. 1) are mainly characterized by a slow negative-positive wave (Engelage & Bischof, 1988, 1989). The negative wave has a large amplitude of up to 700 μV (mean 450 μV, S.E.M. 33 μV) and a latency of about 50 ms (mean 51.4 ms, S.E.M. 1.2 ms). The amplitude of the positive wave is smaller (up to 350 μV) and the latency longer (100–150 ms). Ipsilaterally evoked VEPs usually show only a single negative wave of small amplitude up to 150 μV (mean 84 μV, S.E.M. 7.4 μV) (see Fig. 2). The latency of this wave (mean 63.3 ms, S.E.M. 3.4 ms) is

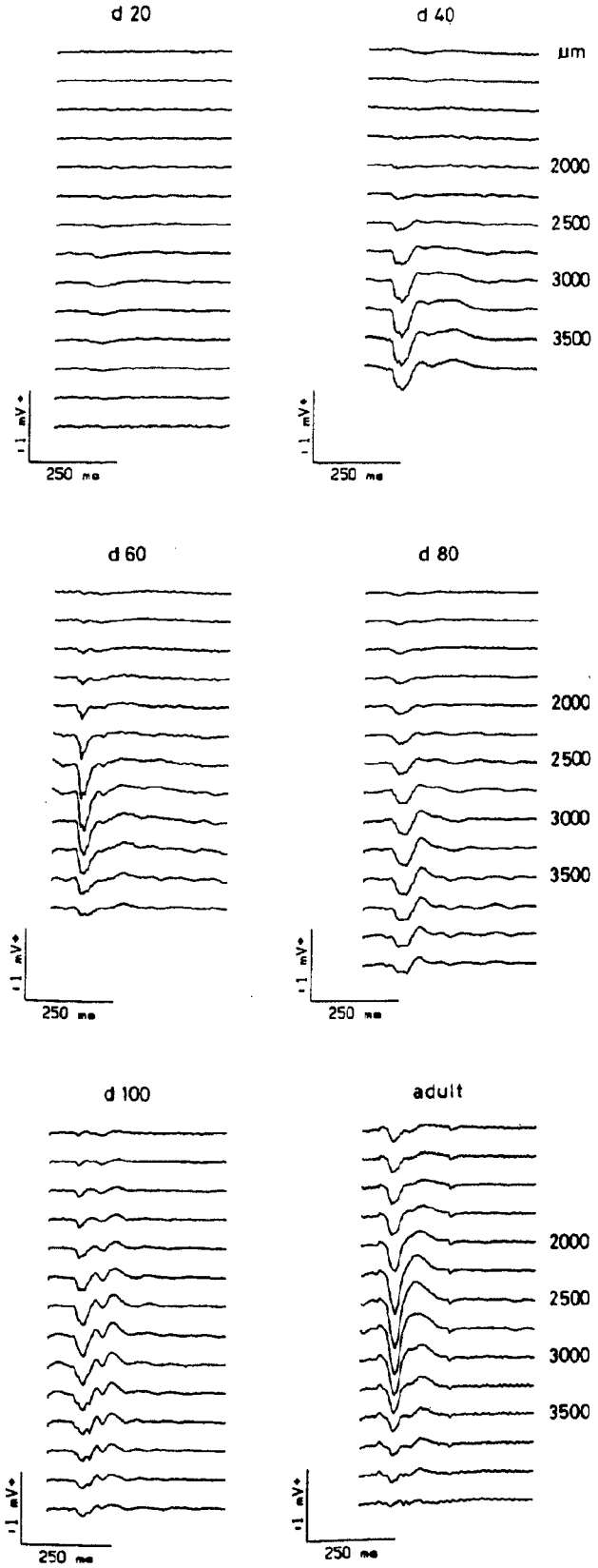


Fig. 1. Development of contralateral VEP responses in the ectostriatal complex of the zebra finch. Electrode tracks referring to the standardized recording coordinates (anterior: 3.15 mm; lateral 3.5 mm; depth 1–4 mm) at days 20, 40, 60, 80, and 100 posthatching and in adult birds.

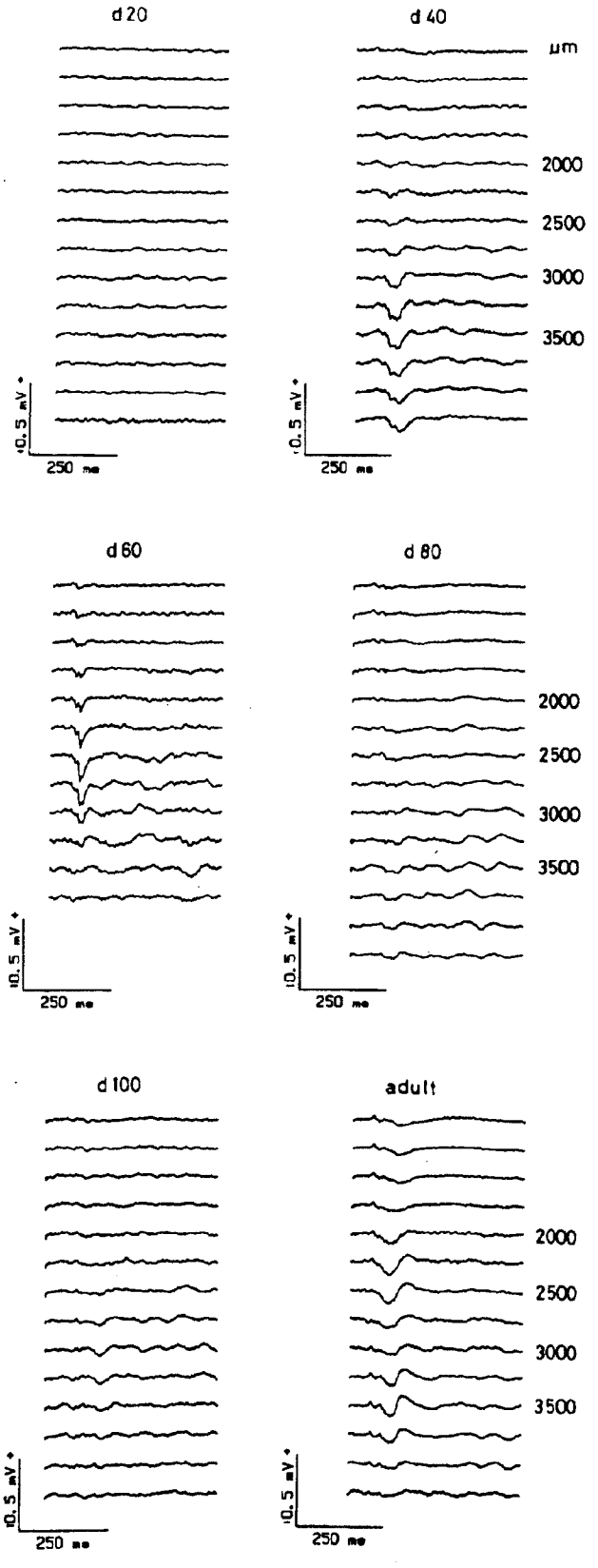


Fig. 2. Development of ipsilateral VEP responses in the ectostriatal complex of the zebra finch. Presentation is as in Fig. 1. Note that ipsilateral VEPs are not present at day 20.

delayed by about 10–15 ms compared to the negative wave of contralateral VEPs (Engelage & Bischof, 1988). In most cases, there is no positive wave detectable in the ipsilateral VEPs.

A CSD analysis of these recordings (Fig. 3) shows a prominent current source (a) at a depth of 1750 μm, slightly above the dorsal border of the ectostriatum. The latency of this source peak is about 50 ms. This early source is followed by a small sink (b) with a latency of about 100 ms. Between 2250 μm and 2500 μm (precisely at the dorsal border of the ectostriatum), the early source reverses into a current sink (a) with two small peaks, and the delayed sink (b) reverses into a source. At 2750 μm, the latency of the early sink (a) shifts from 50–65 ms, while the latency of the delayed source is reduced to about 75 ms. The delayed source reverses into a small sink (c) at 3250 μm. About 250 μm deeper the early sink (a) reverses into a source. Thus, an early source-sink-source pattern with latencies of about 50 ms corresponds to a delayed sink-source-sink pattern with latencies of about 100 ms in the second part.

20-day-old birds

Contralaterally evoked potentials in 20-day-old zebra finches are mainly characterized by a single negative wave of very low amplitude (mean 74 μV, S.E.M. 4.6 μV) and prolonged latency (mean 68 ms, S.E.M. 3.6 ms) compared to the first wave in adult birds. The positive wave is missing or substantially reduced. A clear differentiation of the negative and the positive wave into distinct potential components (as is usually seen in adults) is not a feature of the response at 20 days. In contrast to adults, the VEPs are clearly restricted to the ectostriatal core. The amplitudes ($P \leq 0.00001$, $t = 11.3$) and latencies ($P \leq 0.0001$, $t = 4.3$) of VEPs evoked contralaterally in 20-day-old birds, differ significantly from those evoked in adults. Ipsilateral VEPs were only observed in one out of seven 20-day-old birds. These ipsilateral VEPs are small and only occasionally measurable over a very limited depth area (Fig. 2).

CSD analysis of the contralateral VEPs (Fig. 3) shows a small sink (a) in the ectostriatal core. No clearly detectable source–sink–source sequence as seen in adults can be demonstrated, nor is the delayed sink–source–sink sequence appearing in adults detectable in 20-day-old birds.

40-day-old birds

In contrast to 20-day-old birds, the negative wave of the VEP in the majority of 40-day-old birds is composed of two distinct peaks. Additionally, a low-amplitude (−70 μV) positive wave appears with one or two distinct peaks and a latency up to 200 ms. This pattern closely resembles the waveforms obtained from adult birds. The negative wave reaches a maximum amplitude of up to 400 μV (mean 203 μV, S.E.M. 26 μV) which is similar to several recordings in adults. Although the amplitude distributions of 40-day-old birds and adult birds have a certain degree of overlap, the values from 40-day-old birds differ significantly from those of 20-day-old birds ($P \leq 0.0001$, $t = 4.96$) and adult birds ($P \leq 0.00001$, $t = 5.9$). The latency distributions of the negative wave are similar in 40-day-old birds (mean 45.4 ms, S.E.M. 1.9 ms) and adults ($P \leq 0.05$, $t = 2.7$), but differ significantly from those of 20-day-old birds ($P \leq 0.00001$, $t = 5.5$) (Figs. 4, 5).

In contrast to the recordings in 20-day-old birds, ipsilateral VEPs are consistently detectable in 40-day-old birds in each

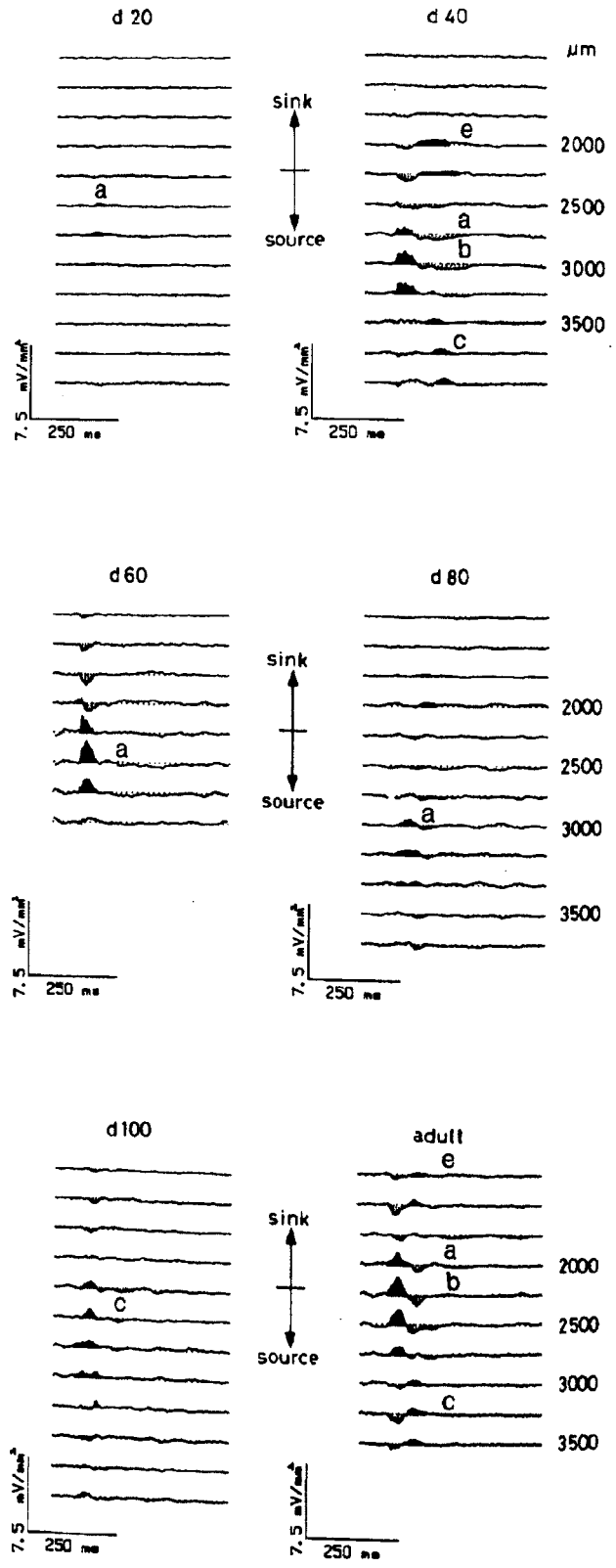


Fig. 3. Development of contralaterally evoked CSD depth profiles in the ectostriatal complex of the zebra finch. Presentation is as in Fig. 1.

case reaching amplitudes up to −150 μV (mean −65 μV, S.E.M. 13 μV) (Figs. 4,5). The latencies are around 50 ms (mean 52.7 ms, S.E.M. 2.7 ms). These values are not significantly different from those in adult birds (amplitudes: $P \geq 0.1$, $t = 1.3$; latencies: $P \leq 0.05$, $t = 2.4$) (Fig. 3).

The CSD analysis of these potentials reveals that the depth profile of 40-day-old birds largely resembles that of adult birds. As in adults, the prominent central current sink (a) appears within the ectostriatal core. This central current sink (a) is dorsally and ventrally surrounded by temporally corresponding current sources. In contrast to 20-day-old birds, the delayed dorsal and ventral sinks (e, c), which are prominent features of the adult CSD depth profile, are present in 40-day-old birds; however, these delayed sinks and sources are of very low frequency, of small amplitude, and not as consistent as in adult birds.

60-day-old birds

In 60-day-old birds, contralateral and ipsilateral VEPs are observed as in 40-day-old birds and adults; however, the contralaterally evoked VEPs in 60-day-old birds represent an intermediate stage between 40-day-old birds and adults in several aspects. Compared to 40-day-old birds, the negative wave is sharpened, its duration is reduced, and its amplitude increased. The pronounced long-latency positive wave, which is clearly detectable in adults, has not yet developed. As in 40-day-old birds, a slow long-lasting positive wave of low amplitude (about 100 μV) with one or two different peaks and latencies around 150 ms is detectable in 60-day-old birds. The amplitude of the negative wave (mean 365 μV, S.E.M. 24 μV) is between that of 40-day-old birds and adults. It differs significantly from that of 40-day-old birds ($P \leq 0.0001$, $t = 4.6$) but not from that of adult birds ($P \leq 0.05$, $t = 2.1$). Latencies of contralateral VEPs as well as amplitudes and latencies of ipsilateral VEPs do not differ significantly from either adults or 40-day-old birds (Figs. 4,5).

The current-source-density depth profiles (Fig. 3) in 60-day-old birds are comparable to those of 40-day-old birds. An early source–sink–source is demonstrated in the CSD depth profiles. The delayed sink–source–sink as in 40-day-old birds remains sluggish and of small amplitude (Fig. 3).

80-day-old birds

Contralaterally evoked VEPs for 80-day-old birds differ markedly in one respect from those of 60-day-old birds and adults. The amplitude of the negative wave (mean 155 μV, S.E.M. 12 μV) is dramatically reduced compared to 60-day-old birds, and is well below that of adult birds. These differences are highly significant (day 80 *versus* day 60: $P \leq 0.00001$, $t = 7.9$ and day 80 *versus* adults: $P \leq 0.00001$, $t = 8.4$). There is, however, no significant difference when compared to 40-day-old birds ($P > 0.05$, $t = 1.7$). No significant differences can be observed between day 60, day 80, and adult birds with respect to the latencies of the negative wave of the contralaterally evoked VEPs, and the amplitudes and latencies of ipsilaterally evoked VEPs (Figs. 4,5). Indeed, no obvious qualitative differences are detectable between VEPs of 80-day-old birds and adults besides the drastic reduction in the amplitude of the negative wave in the contralaterally evoked VEP.

In the current-source-density depth profiles (Fig. 3), the central sink (a) and its corresponding current sources are easily detectable, although the amplitudes are very small. The delayed sink–source–sink sequence is not very prominent.

100-day-old birds

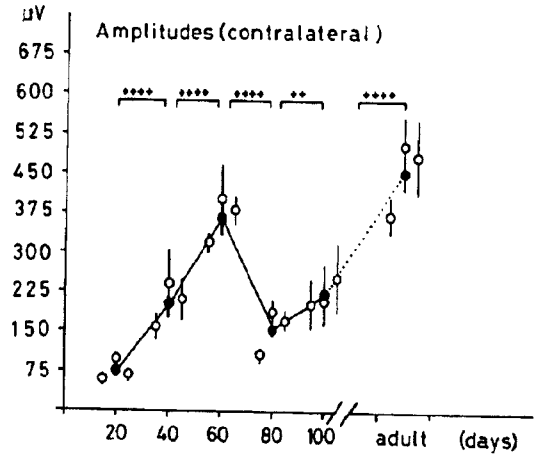
Contralaterally evoked VEPs from 100-day-old birds differ from those of 80-day-old birds and adults. The amplitude of the negative wave is enhanced (mean 221 μV, S.E.M. 12 μV) compared to 80-day-old birds, but is still clearly below that of adult birds. These differences are significant (day 80 *versus* day 100: $P \leq 0.001$, $t = 3.9$ and day 100 *versus* adults: $P \leq 0.00001$, $t = 6.5$). However, as in 80-day-old birds there are no significant differences when compared to 40-day-old birds ($P > 0.05$, $t = 0.6$). No significant differences could be observed between the latencies of the negative wave of the contralaterally evoked VEPs, and the amplitudes (Fig. 4) and latencies (Fig. 5) of ipsilateral evoked VEPs when comparing 100-day-old birds to adults. As in 80-day-old birds, no qualitative differences are detectable in the VEPs if compared to adults.

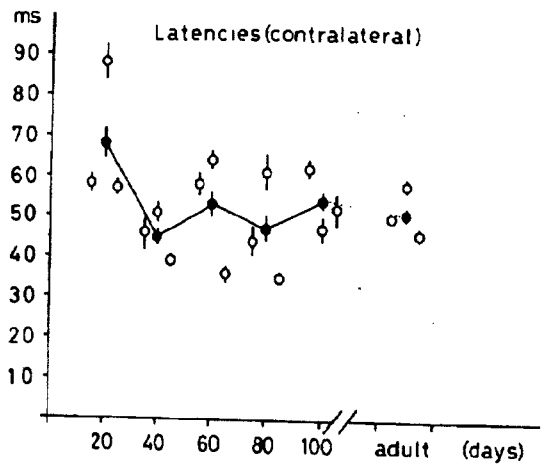
In the current-source-density depth profiles (Fig. 3), the central current sink (a) and its corresponding current sources are easily detectable, although the amplitudes are very small. The delayed sink–source–sink sequence is still not very prominent.

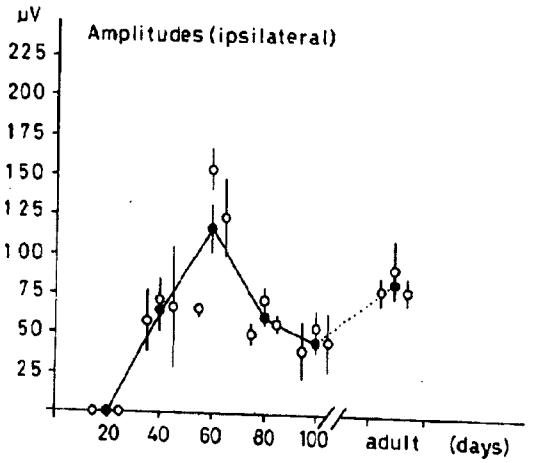
Discussion

Our earlier investigations in the zebra finch, an altricial bird, showed that the morphological development of visual target areas is mainly characterized by a rapid increase in neuronal size (Herrmann & Bischof, 1987*a*,*b*) along with other morphological parameters such as increasing dendritic spine density and dendritic arborization until day 20 (Herrmann & Bischof, 1988*b*). After day 20, cell bodies become progressively smaller (peak-decline trend) until nearly adult cell sizes are reached at day 40. A similar pattern is seen in the development of target area volume (Herrmann & Bischof, 1988; Nixdorf, 1986) as well as in synapse density, presynaptic terminal size, and length of postsynaptic thickening in the thalamic nucleus rotundus and the ectostriatum of the zebra finch (Nixdorf & Bischof, 1986; Nixdorf, 1986). Some parameters continue to change until adulthood. However, the anatomical changes after day 40 are generally not statistically significant (Herrmann & Bischof, 1986*a*, 1988*a*). In contrast, the tectofugal visual pathway does not respond to visual stimuli in the same way as in adult birds of this age. The physiological data presented above clearly demonstrate that only changes in the latency distribution of VEPs reach adult values at 40 days. Whereas the latencies recorded in 20-day-old birds are significantly longer than those in 40-day-old birds, no further significant decrease can be observed in the subsequent age classes. The decrease of latencies until day 40 may be explained by anatomical findings that demonstrate that at day 20 the myelination of fibers in the tectofugal system of the zebra finch is still incomplete, reaching adult densities at day 40 (Herrmann & Bischof, 1986*a*). The latencies of the VEPs are likely to be dependent on the increase of nerve conduction velocity, a consequence of the increasing myelination of the afferent fibers.

In contrast, the VEP shapes, current-source-density depth profiles, and amplitude distributions are clearly not adult-like at day 40. A comparison of contralaterally evoked visual re-







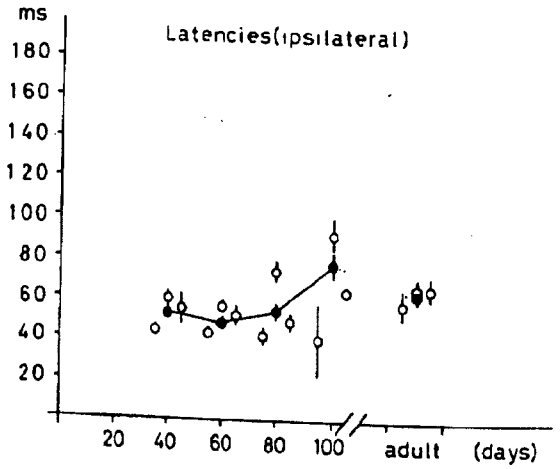


Fig. 4. Mean (±S.E.M.) of the amplitudes of contralateral and ipsilateral VEPs in the ectostriatal complex of the zebra finch at different ages. Open circles: Mean (±S.E.M.) of contralateral VEPs of individual birds ($n = 7$ for each point). Closed circles: Mean (±S.E.M.) of contralateral VEPs of pooled data from three birds. The amplitude values of contralateral evoked VEPs show a nearly linear progression up to day 60. All differences in the amplitude values in succeeding age classes are statistically significant. A comparison of 40- to 80-day-old birds and 60-day-old birds to adults reveals no significant differences ($P > 0.05$). Besides the fact that ipsilateral VEPs are not present at day 20, no significant differences can be demonstrated in the development of ipsilateral VEPs. Note the coincidence of high amplitudes in contralateral and ipsialteral VEPs at day 60. From day 60 to day 80, a dramatic decrease in the contralateral VEP amplitude occurs. The contralateral VEPs then recovers from about day 100. ++++: $P < 0.00001$; ++: $P < 0.001$ (two tailed Student's t-test).

Fig. 5. Mean (±S.E.M.) of the latencies of contralateral and ipsilateral VEPs in the ectostriatal complex of the zebra finch at different ages. Presentation is as in Fig. 4. No ipsilateral response was present in 20-day-old birds. Only the latencies of contralateral VEPs in 20-day-old birds are significantly prolonged compared to all other age groups ($P < 0.00001$, two-tailed Student's t-test). All other differences in latency values are not statistically significant.

sponses in 20-, 40-, and 60-day-old birds demonstrates an almost linear increase. These data demonstrate that the time period over which physiological changes occur in the course of development of the ectostriatum clearly exceed the anatomical development.

There are several mechanisms that could contribute to the observed increase in VEP amplitude with age. The above-mentioned improvement in myelination may lead to a more uniform conduction velocity in the afferent fibers and therefore to a better time locking of the responses to the stimulus. This in turn should enhance the amplitude of the evoked responses in the ectostriatum. A second mechanism is related to the process of neuronal specialization. Theories of developmental processes are commonly based on the assumption that many redundant, not yet functionally verified, intercellular connections exist in juvenile brains (e.g. Changeux & Danchin, 1976). In zebra finches, the size of neurons and the number of spines in the ectostriatum decrease after day 20 (Herrmann & Bischof, 1988*a*). This exuberant connectivity leads to a largely random distribution of current flow vectors and therefore a strong cancellation of currents (e.g. Llinas & Nicholson, 1974; Mitzdorf, 1985). Because of this cancellation of currents only a small low-frequency VEP response is evoked in the ectostriatum. With increasing specification of the neuronal networks during development, the cancellation of currents decreases, macroscopic current sinks become larger, and consequently the VEP responses are enhanced.

Concerning the development of ipsilateral VEPs in the ectostriatum, there were no significant differences between amplitudes of latency distributions between 40-, 60-, and 80-day-old birds and adults. There was, however, one very important qualitative

result. In 20-day-old birds, we were able to demonstrate reliable contralateral VEPs but no ipsilateral VEPs. This shows that ipsilateral stimulus processing in the ectostriatum develops about 20 days later than contralateral stimulus processing. Whether this delay has effects on the development of binocular processing in birds is not yet known. Interestingly, recent data from our laboratory concerning the development of the visual wulst demonstrate that the ipsilateral influence on this area is substantially reduced between day 20 and 40 (Bredenkötter & Bischof, submitted). It might be possible that in laterally eyed birds the tectofugal pathway takes over the task of binocular processing from the thalamofugal pathway at this age.

The most puzzling finding in the present experimental data is the interruption of the linear increase in the development of VEP amplitude in 80-day-old birds. While the amplitude of the response in 60-day-old birds does not differ significantly from adult values, the amplitude in 80-day-old birds is significantly smaller than that of both 60-day-old birds and adults, being similar to that of 40-day-old birds. This dramatic decrease in the visual responsiveness of the ectostriatum clearly occurs after the termination of neuroanatomically detectable changes in the natural development of this pathway.

Therefore, from an electrophysiological point of view, it is by now difficult to define a point in the natural development from which an animal can be judged to be an adult bird. Morphological features, such as plumage, size, and weight of the birds allow no clear distinction of different ages after day 80. There is, however, one morphological criterion which correlates well with the results of the present study. The pneumatization of the cranium reaches adult characteristics not before 150 days of age (Serventy et al., 1967). All recordings made from birds with complete pneumatization of the cranium were adult-like with respect to maximum amplitude, latency, and potential shape. In the present study, all birds included in the adult group showed a complete pneumatization of the cranium.

At present, we do not have a fully conclusive interpretation for decrease in VEP amplitude at 80 days of age. There are several different physiological processes that may induce this late decrease in the visual responsiveness of the ectostriatum. For example, around day 80 a massive increase in the production of steroid hormones such as testosterone, progesterone, and estradiol, has been demonstrated (e.g. Pröve, 1983). This might interfere with the development of the ectostriatal responsiveness to visual stimuli. Likewise, this age coincides with the development of the courtship chain, a complex visually guided behavior in zebra finches (Bischof, 1985, 1988). However, we do not see any direct connection between these events and the decrease of the evoked potentials.

A much more convincing explanation for the delayed decrease in visual responsiveness (between day 80 and 100) is given by the idea of a second wave of progressive events in the ectostriatum. Following the same line of argument already employed in the explanation of the increasing responsiveness of the ectostriatum during development (see above), the decrease in responsiveness around day 80 may be explained by a second delayed wave of invading fibers which disrupt the originally established pattern of connectivity, leading to desynchronization of the ectostriatal neuronal network, and therefore a decrease in VEP amplitude. This would then be followed by a second period of stabilization of the connectivity of these fibers in the ectostriatum. A model describing the stabilization of inbalanced excitatory inhibititory networks has been elaborated by Changeux and Danchin (1976). The invading fibers may originate in the second telencephalic target area of the visual system, the visual wulst, in which the visual responsiveness to ipsilateral stimuli declines during this time (Bredenkötter & Bischof, submitted). Anatomical (Ritchie & Cohen, 1977) and electrophysiological (Engelage & Bischof, submitted) data demonstrate the existence of this cortico-cortical projection. However, nothing is known on the development of this projection.

An anatomical study by Herrmann and Bischof (1988) demonstrated that a second peak of enhanced sensitivity to external stimuli occurred when the birds were visually deprived from day 40 to day 80. The end of this deprivation period coincides temporally with the remarkable decrease in the visual responsiveness of the ectostriatum as seen in the contralaterally evoked VEPs (see Results above). Thus, both studies lead to the conclusion that there is a second time period in the development of the visual system far beyond the early period of life, usually called the "sensitive phase," in which the system is unstable and sensitive to external stimuli. Both events, the second peak of susceptibility to external stimuli and the late decrease in visual responsiveness in the ectostriatum, are far beyond the sensitive phase for sexual imprinting in the zebra finch.

Our experiments demonstrate that the development of the visual system in birds is not a continuous process by which the physiological properties of immature neurons are steadily altered until the adultlike pattern is attained, but rather that discontinuities can be detected with careful observation. Therefore these discontinuities in the development of the visual system may be a common phenomenon that should be considered in future research.

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