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Short Communications

Monocular deprivation affects neuron size in the ectostriatum of the zebra finch brain

KATHRIN HERRMANN and HANS-JOACHIM BISCHOF

Universität Bielefeld, Fakultät für Biologie, Lehrstuhl für Verhaltensphysiologie, Bielefeld (F.R.G.)

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The effects of different periods of monocular deprivation on cell sizes in the ectostriatum, the telencephalic relay of the tectofugal pathway in zebra finches, were evaluated. Following 20 days of monocular closure, neurons in the deprived and undeprived hemisphere show an unselective hypertrophy of 10%. Extending the deprivation period results in a shrinkage of neurons of the deprived side to values of adult normally reared birds, whereas the non-deprived neurons maintain their hypertrophied size.

It is widely accepted that early monocular deprivation (MD) in mammals dramatically alters physiology and anatomy of central visual pathways[4,18,24]. Anatomical effects like changes in dendritic spine density[7,23], number and size of synapses[8,26] and number of vesicles[29] have been found in the visual cortex after MD. Moreover, changes in neuron size in the lateral geniculate nucleus (LGN) have been reported in various species[9,10,12,17,25,28]. It is interesting, however, that cell size in the visual cortex seems to be unaffected by such a manipulation[13,27].

In contrast to the mammalian visual system relatively little is known about the effects of MD on the visual pathways in birds. The data available for the thalamofugal system of owls, often believed to be homologous to the geniculostriate pathway in mammals[20], suggest that similar effects can be obtained in birds[22]. We have recently demonstrated (Herrmann and Bischof, submitted) that early monocular lid closure alters the size of neurons in the nucleus rotundus, the thalamic relay of the tectofugal projection. The effects, however, markedly differ from those observed in mammals. In zebra finches, neurons in the deprived nucleus rotundus, i.e. the nucleus receiving input from the contralateral deprived eye, seem to be unaffected by monocular deprivation, whereas neurons in the non-deprived nucleus, driven by the contralateral open eye, show a hypertrophy of about 15%.

In this study we tried to find out whether the effect found in mammals, namely that changes in cell size can only be observed in the thalamus and not in the forebrain, can be demonstrated in birds, too. We therefore examined the effects of MD on neuron size in the ectostriatum, the telencephalic relay of the tectofugal pathway[16,21]. The obtained values are compared with data on cell size of normally reared birds.

Twenty-two zebra finches (*Taeniopygia guttata castanotis*) of both sexes and of different ages from the institute's stock were used for this study. Twelve birds served as controls ('normal') and 10 were monocularly deprived from the first or second day of life, when the eyes are still closed, until sacrifice. The birds were deprived either by glueing a plastic cap onto one eye or by spreading a liquid adhesive plaster over the closed eyelid[5]. The following age groups were studied: 20 days (normal: n = 4, deprived: n = 4), 40 days (normal: n = 4, deprived: n = 3) and at least 100 days of age (normal: n = 4, deprived: n = 3). The birds were perfused via the left ventricle with

Correspondence: K. Herrmann, Universität Bielefeld, Fakultät für Biologie, Lehrstuhl für Verhaltensphysiologie, Morgenbreede 45, Postfach 8640, 4800 Bielefeld 1, F.R.G.

0.9% NaCl, followed by 10% formalin in saline. The brains were processed according to standard histological techniques, cut horizontally into 30-μm thick frozen sections and counterstained with 1% cresyl violet. Cell size in the medial part of the ectostriatal core region was determined by drawing the outlines of cross-sectional areas of neuronal somata with a visible nucleolus within the left and right hemisphere, respectively, at a magnification of $\times$1250 (n = 200 for each bird). The areas were measured on a Hewlett Packard graphics tablet and the data stored and processed by a HP 85 computer. The obtained values were tested for differences using a two-tailed Student's *t*-test. All results of cell size measurements are presented graphically in Fig. 1.

At 20 days

After 20 days of MD neurons in the ectostriatum, which receive their main input mainly from the deprived eye, do not differ significantly from cells in the corresponding non-deprived hemisphere (110.10 $\pm$ 29.0 μm^2 vs 114.30 $\pm$ 31.48 μm^2, Fig. 1). The frequency distribution of neuron sizes of brain AF is shown in Fig. 2. A comparison of the data obtained from the 4 deprived birds and from normally reared birds (100.84 $\pm$ 21.77 μm^2), however, reveals a hypertrophy of about 10% and 12.9% in the deprived and non-deprived hemisphere, respectively.

At 40 days

After 40 days of monocular lid closure there is a marked hemispheric asymmetry in cell size of 18.4%: neurons in the deprived ectostriatum are significantly smaller if compared to their interhemispheric coun-

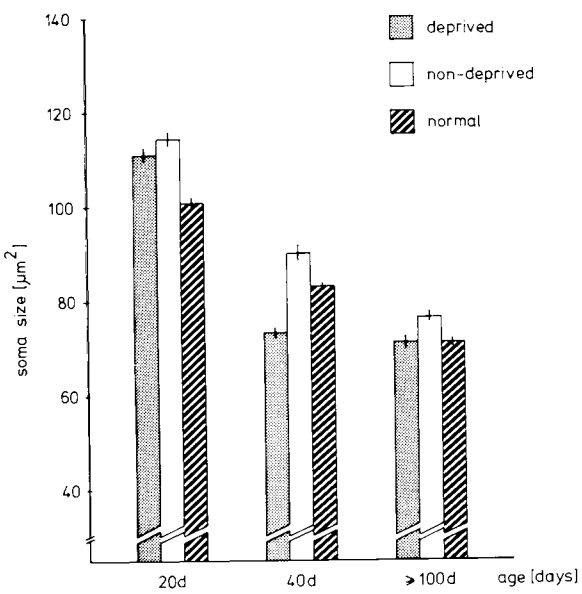

Fig. 1. Comparison of mean cross-sectional areas of ectostriatal neurons of normal and visually deprived (deprived and non-deprived) birds of different ages. Number of cells in each column: n = 400, except for 40- and 100-day-old deprived birds: n = 300. The bars represent the S.E.M. obtained from the pooled data.

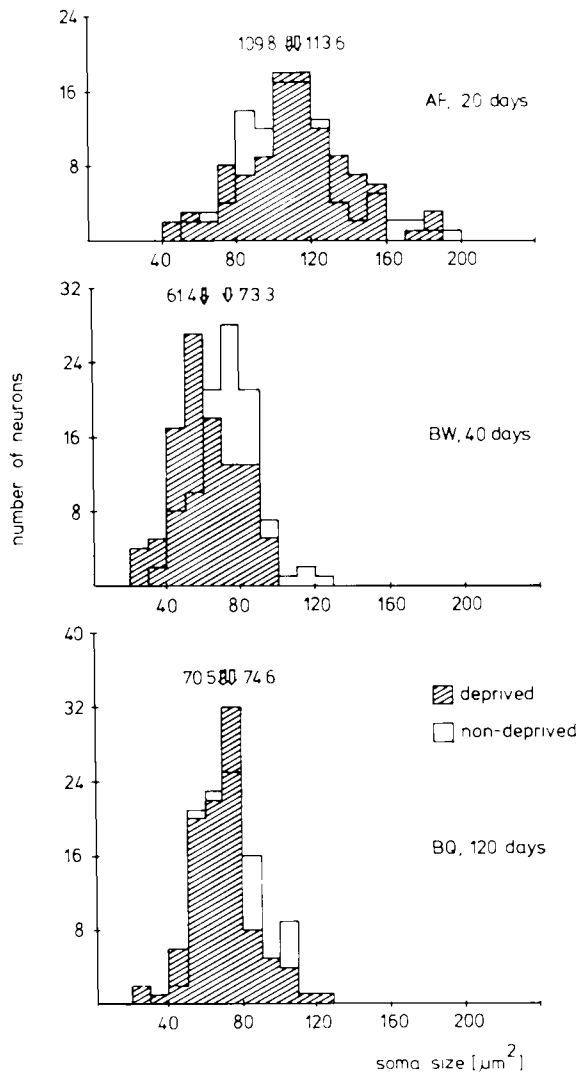

Fig. 2. Frequency histograms showing the distribution of ectostriatal neurons of representative zebra finch brains deprived until sacrifice after 20 days (bird AF), 40 days (bird BW) and 120 days (bird BQ). Each histogram shows the cross-sectional areas of 100 neurons of the deprived (shaded) and non-deprived (white) hemisphere. The open arrows mark the mean value for the cells in the deprived nucleus, the shaded arrows mark mean values for deprived ectostriatal neurons. Column width is 40 μm^2.

terparts (73.33 ± 19.16 μm^2 vs 89.88 ± 27.27 μm^2, $P < 0.0011$, see brain BW in Fig. 2 for example) or to the value they had 20 days before (73.33 μm^2 vs 110.10 μm^2). Correspondingly, the deprived neurons are smaller than ectostriatal cells of normally reared birds (83.04 ± 16.98 μm^2). On the other hand, neurons driven by the open eye, having a size of 89.88 μm^2, are significantly larger than both deprived (+22.6%) and normal somata (+8.2%).

At 100 days or more

Extending the deprivation time up to at least 100 days of age does not seem to affect the deprived cells: they exhibit the same size as neurons of normal birds (71.29 ± 25.76 μm^2 vs 71.12 μm^2), which is the size they already had two months before. On the other hand, neurons receiving input via the open eye show a hypertrophy of 7.9% (76.71 ± 20.59 μm^2) compared to values of normally reared birds. In contrast to the data on cell size following 40 days of monocular closure, where all 3 brains exhibited the same significant interhemispheric asymmetry in ectostriatal cell size, the results after longer periods of deprivation are not as conclusive. The interhemispheric difference is significant for one brain ($P < 0.001$), but less significant for the second ($P < 0.044$) and not significant for the third brain ($P < 0.09$), (e.g. brain BQ in Fig. 2).

This pilot study is the first to provide data concerning the effects of visual deprivation on cell size in the forebrain of birds. Previous studies have dealt with different aspects of MD in birds, e.g. behavioral deficits[5], effects on electrophysiology[22], transmitters[2] and enzymes[1] in the visual wulst, and electrophysiological[3] and ultrastructural[6] changes in the retina, optic nerve and tectum opticum. We have recently demonstrated (Herrmann and Bischof, submitted) that early monocular lid closure alters the size of neurons in the nucleus rotundus, the thalamic relay of the tectofugal pathway in zebra finches.

In normal zebra finches cell size in the ectostriatum, the telencephalic station of this projection, increases during the first 20 days of life and then decreases until adulthood[11]. Our present study clearly demonstrates that this 'peak–decline trend'[19] is also found in deprived birds, but superimposed by two subsequent deprivation effects: after 20 days of MD the neurons of both the deprived and the non-deprived hemisphere show a hypertrophy compared to normal birds of the same age. Prolonging the deprivation period to 40 days of age has different effects, namely that neurons of the deprived side are smaller than in normal 40-day-old birds and have already reached adult size. Neurons in the non-deprived hemisphere are still hypertrophied compared to normal birds. At 100 days of age, cells of the deprived ectostriatum do not differ from normal animals, whereas the hypertrophy of the non-deprived neurons remains.

In summary, after inducing an initial hypertrophy in both hemispheres, MD accelerates the shrinkage of neurons on the deprived side and reduces the shrinkage on the non-deprived side. Hypertrophy on the non-deprived side as a consequence of deprivation has already been described for the LGN of cats[12] (but see ref. 15) and monkeys[10]. This effect could be understood as a reflection of an enhanced physiological activity, accompanied by an increased dendritic and/or axonal arborization[9] (Nixdorf and Bischof, in preparation). In addition we were able to demonstrate such a hypertrophy on the deprived side, which has not been mentioned in other studies. One interpretation may be that this hypertrophy is caused by the attempt of the neuronal circuits to compensate the effects of deprivation by providing additonal synaptic offerings (Nixdorf and Bischof, in preparation), as suggested by Wolff[30]. The rapid shrinkage of neurons to their normal adult size may then be the result of the failure to function adaequately.

In any case, the pattern of changes obtained in this deprivation study suggests interactions between the two hemispheres. In contrast to the thalamofugal system in birds, neither binocular neurons nor competition mechanisms have been described for the tectofugal system. However, tectotectal and tectorotundal interhemispheric projections indicate that such interactions between the two brain sides are possible[14]. The mechanism of the interactions conveyed by these projections is under investigation in our lab (Engelage and Bischof, in preparation).

In contrast to mammals, MD in birds also affects the size of neurons in the telencephalic station of the visual pathway. However, area 17 in mammals and the ectostriatum in birds are non-homologous structures, and comparable studies on the extrastriate projection are not available. Another explanation may be

that the differences in cell size, as in our study, decrease and might disappear finally at a certain age. So far, only deprivation effects on striatal cell size have been investigated in adult monkeys[13,27]. Perhaps MD studies of younger mammals might show the same effect we demonstrated in the zebra finch.

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