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Effects of monocular deprivation in the nucleus rotundus of zebra finches: a Nissl and deoxyglucose study

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Summary. We evaluated in zebra finches the effects of monocular deprivation on morphological and physiological features of the nucleus rotundus, the thalamic relay station of the tectofugal pathway. In a first series of experiments neuron size and total volume were estimated in animals deprived for 20, 40 and at least 100 days and compared to values obtained from normally reared birds. Monocular closure for more than 40 days causes a marked hypertrophy in cells receiving their main input from the open eye, whereas the deprived cells are normal in size. However, with only 20 days of monocular deprivation both deprived and non-deprived rotundal neurons are larger than normal. This indicates that monocular closure has a biphasic effect: firstly, an unselective hypertrophy of deprived and non-deprived neurons, and secondly, a subsequent period of shrinkage of the deprived cells to normal values, while cells driven by the open eye remain hypertrophied. The total volume of the deprived n. rotundus turns out to be smaller in all age groups. In a second series of experiments the activity of the n. rotundus of animals monocularly deprived from birth for 100 days was investigated with the 2-deoxyglucose-method (Sokoloff et al. 1977). With binocular stimulation the activity of the deprived n. rotundus was reduced by about 40%. Depriving adult animals for 100 days does not result in asymmetric labeling of the n. rotundus. We interpretate the 2-DG data as evidence for the existence of a sensitive period for the effects of monocular deprivation. The anatomical data suggest, however, that the effects of monocular deprivation in birds are different from those observed in mammals.

Key words: Monocular deprivation – Visual system – Birds – Neuron size – 2-deoxyglucose

Introduction

The visual system of mammals is one of the best investigated models for the influence of the environment on the development of the nervous system. Since the pioneering work of Hubel and Wiesel in the early sixties ample evidence has accumulated demonstrating that abnormal experience during infancy can drastically and irreversibly alter structural and functional features of central visual pathways (for review see Blakemore 1978; Sherman and Spear 1982; Fregnac and Imbert 1984). Monocular deprivation leads to a severe loss of cells excitable from the deprived eye (Wiesel and Hubel 1963, 1965), if the closure is maintained during the so-called sensitive period. The functional effects are associated with a reduction in the size of ocular dominance columns (Hubel et al. 1977; Le Vay et al. 1980) and with differential shrinkage of cells in the lateral geniculate nucleus (Kupfer and Palmer 1964; Guillery and Stelzner 1970; Guillery 1972; Sherman and Wilson 1975; Vital-Durand et al. 1978; Casagrande and Joseph 1980; Headon et al. 1985).

Most of the physiological and anatomical changes following early unilateral lid closure have been attributed to an unbalanced binocular competition (Wiesel and Hubel 1965; Guillery and Stelzner 1970; Guillery 1972). This interpretation is supported by three findings: first, binocular deprivation causes milder electrophysiological (Wiesel and Hubel 1965) and anatomical effects (Guillery 1973; Hickey et al. 1977; Kalil 1980; but see Vital-Durand et al. 1978; Mower et al. 1985). Second, cell sizes in the monocular or artificially induced "critical" segment are less affected by monocular closure than neurons in the binocular LGN segments (Guillery and Stelzner 1970; Guillery 1972; Von Norden et al. 1974). Third, monocular deprivation in rabbits, mammals with a predominantly monocular geniculocortical pathway,

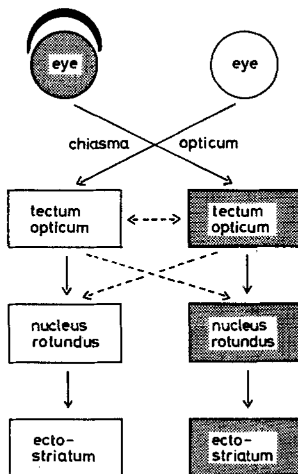

Fig. 1. Monocular deprivation in birds has major effects on the tectofugal structures contralateral to the deprived eye. ⟶ major projections, --→ minor projections

produces less structural and functional changes than visual deprivation in a predominantly binocular pathway (Chow and Spear 1974).

In spite of the large body of literature on the mammalian system, relatively little is known about effects of monocular deprivation in birds. A study by Pettigrew and Konishi (1976), however, demonstrated, that the sensitivity to manipulations of early visual experience of neurons in the visual wulst (probably homologous to the visual cortex) of owls, a species with a large binocular field, resembles that of cats or monkeys. More recent studies on monocular deprivation in the visual wulst of pigeons also suggest similarities to the mammalian visual system (Bagnoli et al. 1982; Burkhalter et al. 1982).

The aim of this study was to determine, whether the nucleus rotundus, the diencephalic relay – station of the tectofugal pathway (Karten 1965; Nixdorf and Bischof 1982) of zebra finches is susceptible to early monocular deprivation. Due to the complete crossing of the retino-tectal connection, nucleus rotundus, probably homologous to the mammalian nucleus lateralis posterior thalami (Nauta and Karten 1970), receives its main input from the contralateral eye (Cowan et al. 1961). Thus, monocular deprivation in the tectofugal pathway creates a deprived hemisphere (contralateral to the deprived eye, shaded in Fig. 1) and a non-deprived hemisphere (ipsilateral to the deprived eye), although there is a minor tectotectal and a small projection form the tectum opticum to the contralateral nucleus rotundus (Benowitz and Karten 1976; Hunt and Künzle 1980) (Fig. 1). However, no binocular neurons have been reported in the tectofugal pathway so far.

We determined cell size and volume differences in birds deprived for various periods, similar to studies on the LGN morphology, and examined metabolic activity of the nucleus rotundus of monocularly deprived zebra finches, using the 2-Deoxyglucose-method.

Material and methods

a. Subjects

27 zebra finches (Taeniopygia guttata castanotis) of both sexes from the institute's stock were used for this study, 22 for the evaluation of cell size and volume, and 5 for the 14C-2-Deoxyglucose (2DG)-experiments. The birds were monocularly deprived (left or right, as described later) on the first or second day of life until they were sacrificed and perfused for anatomical processing. Survival times were 20 ($n = 4$), 40 ($n = 3$) or more than a 100 days ($n = 3$). Furthermore, 20 ($n = 4$), 40 ($n = 4$), and at least 100 day old normally reared zebra finches ($n = 4$) were used as controls.

For the 2DG-study, 2 birds were monocularly deprived from birth to at least 100 days of age and two birds deprived as adults for 100 days. In all birds the lids were reopened under anaesthesia one day before the 2DG-experiment, so that the birds were binocularly stimulated during the exposure. In addition, one bird was monocularly deprived the day before the 2DG-study and then monocularly stimulated during the 2DG-experiment.

b. Lid suture

We used two methods for closing the eyes: for depriving adult animals we usually glued a plastic cap onto one eye, using Dow-Corning Adhesive. Young birds were deprived, beginning at the first or second day of life (before the natural eye opening), either by the same method mentioned above, or by spreading a liquid adhesive plaster (Nobecutan) over the closed eyelids every day, and additionally covering the eye with black eyeliner (Burkhalter and Cuenod 1979). This treatment usually prevents the development of the margin of the eyelid, causing a permanent closure of the eye. These two methods produce essentially the same results, for example bird BW was cap-deprived, whereas BK was Nobecutan-deprived (see results for details).

c. Morphological methods

The birds were deeply anaesthetized with 0.03 ml Nembutal, perfused via the left ventricle with 0.9% NaCl, followed by 10% formaline in saline. The brains were fixed in situ for several weeks and after removal from the scull they were stored in a solution of 30% sucrose in 10% formalin overnight. Frontal serial sections (30 μm thick) were cut and every third section was mounted on gelatine-coated slides and stained with 1% cresylviolet. For the cell measurements of the nucleus rotundus the outlines of 100 neurons showing a visible nucleolus were drawn at a magnification of 800 ×, using a drawing tube attached to a Zeiss microscope. Cells were sampled from the most medial part (in rostro-caudal as well as in mediolateral direction), excluding the dorsal part, the so-called triangularis, and the ventral part of the nucleus, which does not receive tectal efferences but input from the SP and IPS (Benowitz and Karten 1976). The cross-sectional areas were determined using a Hewlett Packard Graphics Tablett attached to a HP 85 microcomputer. From the stored data the means, medians

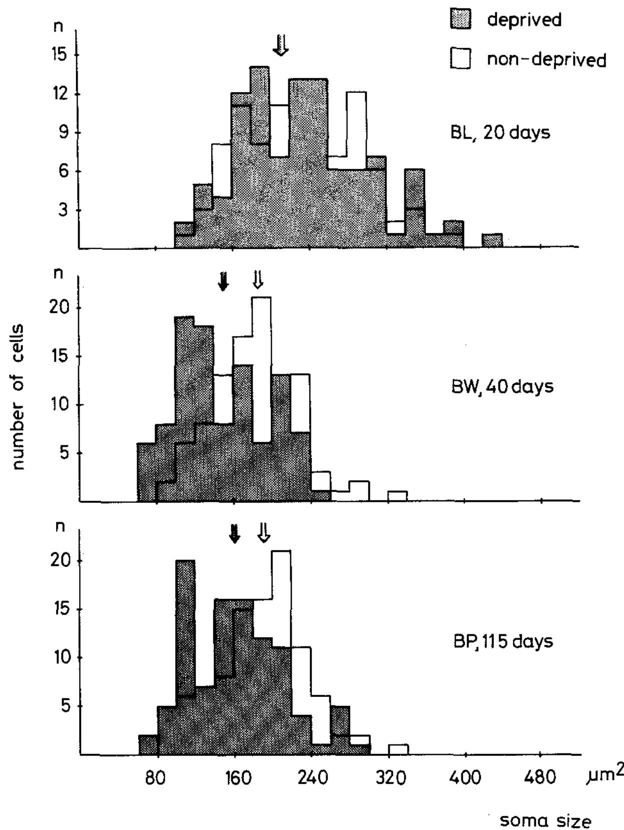

Fig. 2. Frequency histograms showing the distribution of nucleus rotundus cells of representative zebra finches deprived till sacrifice after 20 days (bird BL), 40 days (BW) and 115 days (BP). Each histogram shows the cross sectional areas of 100 cells in the deprived (shaded) and non-deprived (white) hemisphere. The open arrows mark the mean value for the cells in the non-deprived nucleus rotundus, the shaded arrows mark mean values for deprived rotundal neurons. Bin width is 40 µm²

and standard deviations were computed and statistical comparison between cell sizes was performed by using a two-tailed t-test and Mann-Whitney U-test. The second test was applicated as at least some of the distributions were eventually not normally distributed. However, means and the median values were always identical (the difference never exceeded 2%). To make the results comparable to others, we present the t-test data here, as this test is used much more frequently in comparable studies. To determine the volume of the n. rotundus the cross sectional area of the total rotundal surface was estimated in every third 30 µm section in the same way as for cell measurements, but at a magnification of × 79. The obtained areas were multiplied with 90 µm and the volume slabs were added up. No adjustments were made for tissue shrinkage, as it proved to be rather constant at all ages.

d. The 2DG-method

The birds were given 0.12 µCi 14C-2-Deoxyglucose (2DG) in 0.05 ml 0.9% NaCl intramuscularly and allowed to view the laboratory scene for 60 min. Then the birds were decapitated, the brains were quickly removed and rapidly frozen at −60° C directly on the microtome head. On the following day the brains were cut horizontally at 30 µm in a cryostat at −17° C. The sections were dried on a hot plate at 60° C, and exposed for 4 weeks using a Kodak X-ray film. The autoradiographs were developed in Kodak X-ray developer. The densitometric analysis was performed using a digital image processor. It consisted of a TV camera based digitizer, whose output was connected to a PDP-Computer system. Interhemispheric differences in the rotundus activity were assessed by comparing the relative activity of the deprived with that of the non-deprived hemisphere. Relative activity was expressed as the ratio of the mean optical density of all rotundus sections over the optical density of field L of the same hemisphere. Due to the constant noise-level in the lab, Field L, the telencephalic relay of the auditory pathway in birds, was uniformly labelled in all experiments.

Results

a. Cell size

Table 1 shows the means and standard deviations of the cross-sectional areas of nucleus rotundus cells in experimental animals (deprived and non-deprived hemisphere) and normal zebra finches at different ages. In both, normal birds and deprived animals, cell size decreases from day 20 to day 100. This confirms the results of an earlier study (Herrmann and Bischof 1986) and will not be discussed here. After 20 days of monocular closure there is no significant difference in the mean cell size between deprived and non-deprived nucleus rotundus (231.5 vs 233.5 µm²).

The frequency distribution of neuron size of brain BL in Fig. 2 shows this total overlap of deprived and non-deprived rotundal cells. Following 40 days of monocular deprivation, the differences between deprived and undeprived cells varied between 7.7% and 18.9%, with a mean of 14.9%. Neurons innervated by the closed eye were significantly smaller than cells in the non-deprived nucleus rotundus (176.1 vs 205.8 µm²). A typical example of rotundal soma size distribution after 40 days of monocular closure is presented in Fig. 2 (brain BW). Prolonging the deprivation duration over 100 days or more does not cause further changes: neurons driven by the deprived eye are 15.5% smaller than their contralateral counterparts (162.8 vs 192.6 µm²). See brain BP in Fig. 2 for example.

A comparison between rotundal cell sizes of 20 day old experimental birds with those of normally reared zebra finches indicates that cells in the latter are about 11% smaller than cells in both the deprived and the non-deprived nucleus of the experimental animals (Fig. 3, Table 1: 208.8 vs 231.5/233.5 µm²). With 40 days of monocular closure, cells in the deprived nucleus rotundus are only little affected, as the mean cell size is only 4.9% larger in normal birds

Table 1. Cell size

	Normal n		Deprived d		Non-deprived n–d	% Change d vs n–d	% Change d vs n	% Change n–d vs n
20d	M52	212.82 ± 6.04	AP	278.08 ± 8.67	278.17 ± 8.65	– 0.03		
	M51	222.11 ± 5.12	AF	212.74 ± 5.75	218.16 ± 5.83	– 2.48		
	M53	209.98 ± 4.81	BL	233.82 ± 6.78	234.10 ± 6.18	– 0.12		
	M54	190.48 ± 4.98	AE	201.29 ± 6.49	203.67 ± 6.50	– 1.17		
	total	208.84 ± 3.79	total	231.48 ± 3.37	233.52 ± 3.70	– 0.87	+10.84***	+11.82***
40d	M59	164.41 ± 4.83	BW	149.12 ± 4.64	183.78 ± 4.38	–18.86***		
	M60	183.65 ± 4.93	AT	176.13 ± 4.33	190.75 ± 4.91	– 7.66*		
	M63	181.99 ± 4.91	BK	200.01 ± 5.14	242.87 ± 6.22	–17.65***		
	M100	206.58 ± 4.29						
	total	184.16 ± 2.51	total	175.09 ± 3.16	205.80 ± 3.42	–14.92***	– 4.93	+11.75***
≤ 100d	M85	130.83 ± 3.20	BE	154.70 ± 5.15	186.38 ± 3.94	–17.00***		
	M14	154.23 ± 4.66	BQ	171.68 ± 5.15	204.25 ± 5.25	–15.95***		
	M27	176.94 ± 4.68	BP	162.08 ± 4.93	187.13 ± 4.79	–13.39**		
	M78	178.40 ± 4.51						
	total	160.10 ± 2.49	total	162.82 ± 3.03	192.59 ± 2.85	–15.46***	+ 1.70	+20.29***

* $p < 0.01$
** $p < 0.001$
*** $p < 0.0001$

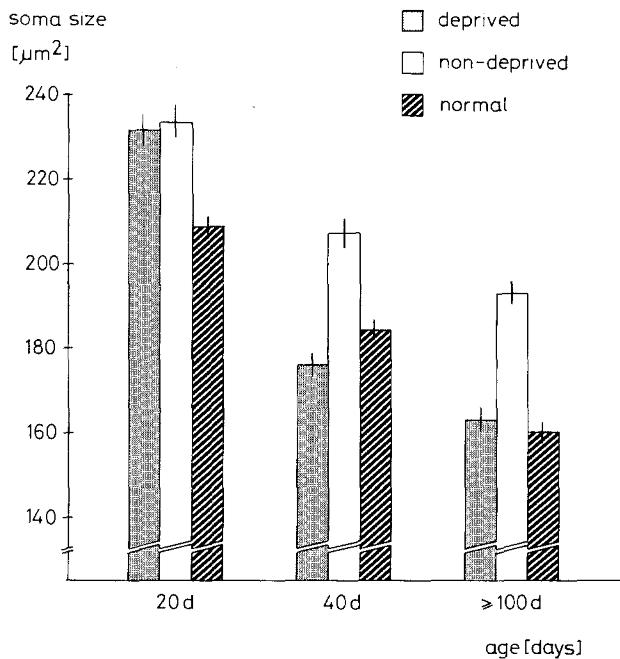

Fig. 3. Comparison of mean cross sectional areas of nucleus rotundus cells of normal and visually deprived birds (deprived and non-deprived) of different ages. The number of cells in each column is n = 400, except for 40 and 100 day old deprived birds: n = 300. Each bar represents the standard error of the mean obtained from the pooled data

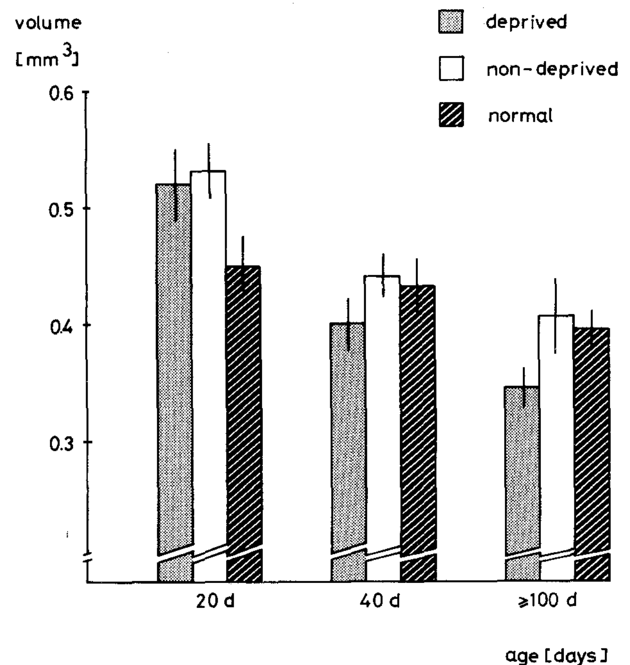

Fig. 4. Volume of deprived and non-deprived nucleus rotundus following different times of monocular closure in comparison to volume values of normally reared birds

than in the deprived rotundus (184.2 vs 175.1 µm^2), and this difference is only weakly significant ($p < 0.02$, t = 2.11, df = 792). In normal adult birds cell sizes are exactly the same as in the deprived rotundus of birds deprived for 100 days (160.1 vs 162.8 µm^2). The undeprived cells, however, are markedly hypertrophied: After 40 days of deprivation they are 11.8% (205.8 vs 175.1 µm^2), and after more than 100 days of deprivation they are 20.3% (192.6 vs 160.1 µm^2) larger than in normal animals.

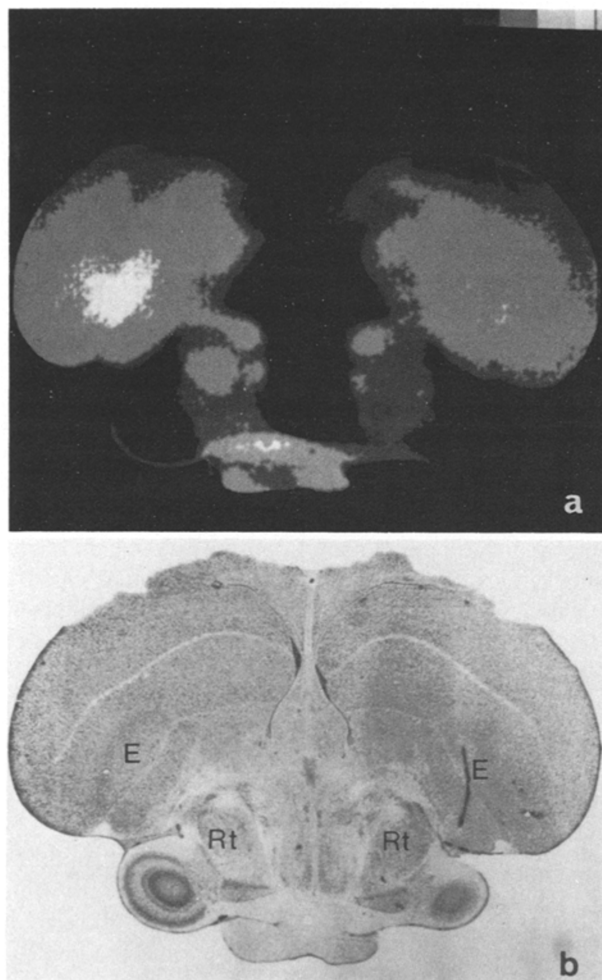

Fig. 5. a Computer generated densitometric plot of an autoradiograph (divided into 4 relative density classes) of bird G4, deprived from birth to day 100. The deprived Rt (right hemisphere) shows a weaker DG-labelling. **b** Corresponding Nissl-section. Rt = n. rotundus, E = ectostriatum

b. Volume

The volume of nucleus rotundus undergoes the same changes with monocular deprivation as the cell size. The difference of 2.75% between deprived and non-deprived rotundus volume following 20 days of monocular closure is milder (0.520 vs 0.532 mm^3) than that observed after 40 (8.5%, 0.401 vs 0.439 mm^3) or 100 days of monocular deprivation (13.7%, 0.351 vs 0.406 mm^3). The difference between deprived and non-deprived rotundus volume of 40 and 100 day old birds is significant at the 0.02% level (Wilcoxon signed rank-test for matched pairs). The volumes of normal rotundus is 0.450 mm^3 for 20 day old birds, 0.443 mm^3 for 40 day old zebra finches, and 0.396 mm^3 for adult birds (at least 100 days).

c. 2-deoxyglucose

Monocular deprivation for the first 100 days of life leads to decreased glucose consumption in the nucleus rotundus contralateral to the deprived eye. In brain G12 the difference of relative optical density between deprived and undeprived hemisphere was 47%, G4 revealed a weaker asymmetry of about 34%. In both cases the difference between the optical density of left and right (or deprived and non-deprived) nucleus rotundus is highly significant (0.001, t-test). Thus, the optical density of the nucleus rotundus driven by the deprived eye is decreased by about 40% (Fig. 5).

In contrast, in birds deprived as adults (G17 and G32) labelling of the deprived and undeprived nucleus rotundus is similar. The slightly higher labelling of the deprived nucleus is not significant.

In a normally reared bird (G27) that was stimulated monocularly the optical density was 61% lower on the side contralateral to the covered eye.

Discussion

The observed changes in rotundal cell size following monocular closure can be described in two ways: either by comparing deprived cells with those of the non-deprived nucleus rotundus of the same animal or by comparing the cell sizes of the experimental brain structures with those of normally reared birds (Headon et al. 1985). Using cells in the corresponding non-deprived nucleus rotundus of the same animal as a control, our results show that after 40 or 100 days of monocular deprivation neurons in the deprived nucleus rotundus are 15% smaller than those in the non-deprived hemisphere. Analysing our data this way, our results are in close agreement with findings in the visual system of mammalian species with large binocular fields (Guillery and Stelzner 1970; Sherman and Wilson 1975; Hickey et al. 1977; Vital-Durand et al. 1978; Casagrande and Joseph 1980; Tigges et al. 1984), although the size differences expressed as percentage between deprived and undeprived cells in cats, monkeys, squirrels and dogs are about twice as high as those observed in zebra finches. After a shorter deprivation time of 20 days, however, there are no differences in cell size between the two hemispheres. Therefore, one would conclude, that 20 days of monocular deprivation is too short a time to produce any cell size changes. This observation of delayed response to monocular closure is consistent with findings of Chow and Spear (1974) in the rabbit visual system, who also failed to find cell size changes after short-term lid suture in this species with small binocular visual field. The

time necessary to produce LGN neuron size changes in this species is several months and hence much longer than in zebra finches. Moreover, the deprivation effects in rabbits are much weaker than in other species including zebra finches (differences between 4.6 and 9.8%).

Some unexpected points emerged when the deprived animals were compared to normally reared birds. As Fig. 2 shows, there is a marked hypertrophy of both deprived and non-deprived rotundal cells following 20 days of monocular deprivation. Up to now we have no conclusive explanation for this finding, which to our knowledge has not been reported in the mammalian visual system following monocular closure.

One interpretation might be that the transient uncrossed retinofugal projection is maintained or strengthened as it has been demonstrated after enucleation in chicks (O'Leary and Cowan 1980). Unfortunately, the existence and time-course of such a projection is only established for precocial, not for altrical birds like the zebra finch. It remains to be determined whether such persistence could also account for changes in the non-deprived hemisphere. Another interpretation might be that the tecto-tectal and/or the contralateral tecto-rotundal projection, mentioned above as a minor pathway, gains functional importance in the deprived birds. We have evidence from electrophysiological data (Engelage and Bischof in prep) for this second interpretation. Longer deprivation causes a hypertrophy in the cells receiving their main input from the open eye and has no effect on the deprived cells. However, a comparison of cell sizes of the deprived nucleus rotundus of 40 day old birds with neuron size values of normal zebra finches demonstrates a 4.6% shrinkage of the deprived neurons. With regard to the small number of samples we neglect this difference, which anyhow is not significant at the 99% level. Thus it appears, that the difference in pericaryal size between the deprived and the non-deprived nucleus rotundus pertains almost entirely to a hypertrophy of neurons receiving input from the open eye. Unfortunately, only little information on interindividual comparison is available. Hickey et al. (1977) obtained the first direct evidence of a hypertrophy in the deprived LGN laminae by comparing neuron sizes from normal cats with those from monocular deprived animals (but see Hoffman and Holländer 1978 and Kalil 1980 in the same species). A recent detailed study of Headon et al. (1985) on morphological changes in rhesus monkeys following monocular deprivation confirms these results. These authors also found that early deprivation initially causes growth of cells in the undeprived parvocellular laminae rather than failure of growth or shrinkage of cells in the deprived laminae. Following longer periods of deprivation in the primate, measurements of LGN neurons reveal shrinkage affecting both deprived and undeprived parvocellular cells (Headon et al. 1985).

In conclusion, then, in zebra finches the permanent hypertrophy of cells in the non-deprived nucleus rotundus and the absence of shrinkage in the deprived nucleus contrasts sharply with the effects of monocular deprivation in mammals. Considering the time-course, monocular deprivation in zebra-finches seems to have a biphasic effect: first, an unselective hypertrophy of deprived and undeprived neurons, and secondly a subsequent shrinkage of the deprived cells to normal values, while neurons driven by the open eye stay hypertrophied.

As mentioned above, there is now extensive support for the existence of competitive mechanisms underlying cell size changes after monocular closure (for review see Sherman and Spear 1982), as neurons in the monocular and "critical" part of the LGN are less affected than somata in the binocular LGN laminae (Guillery and Stelzner 1970; Garey et al. 1973; Sherman and Wilson 1975; Hickey et al. 1977; Casagrande and Joseph 1980). According to a hypothesis put forward by Guillery (1972, Guillery and Stelzner 1972) the soma size of a neuron is a reflection of its axonal arborization and the number of synapses (Tieman 1984). In line with this hypothesis is the close correlation between the size of ocular dominance columns in area 17 and the geniculate cell size after monocular deprivation, which has been shown in a variety of studies (Hubel et al. 1977; Le Vay et al. 1980; Swindale et al. 1981; Tigges et al. 1984).

Unfortunately, this evidence has only limited value for the interpretation of our results. Thus, we do not know whether binocular competition is at all relevant. Despite the discovery of the small contralateral tecto-rotundal projection (Benowitz and Karten 1976), there are yet no hints for binocular mechanisms in this thalamic nucleus.

The interpretation of the 2DG results poses fewer problems. The decreased activity of the non-stimulated rotundus of the monocularly stimulated normal bird G27 confirms earlier results in the pigeon (Streit et al. 1977) and the falcon visual system (Bagnoli and Francesconi 1983). This indicates that the 2DG method is well suitable for the measurement of activity in the visual system of birds.

The decreased optical density of the early deprived nucleus rotundus is thus likely to reflect decreased neuronal activity and thus might reflect a failure to adaequately respond to visual stimulation. This result is in accordance with a 2DG study of

area 17 of squirrel monkeys (Tigges et al. 1984) after monocular deprivation. The decreased optical density of the deprived nucleus rotundus in zebra finches, however, is in contrast to deprivation studies in pigeons: Burkhalter et al. (1983) reported no asymmetries in 2DG activity in the tectofugal pathway after early monocular deprivation. As the interhemispheric difference in DG-consumption in the pigeon study was not expressed quantitatively, the differences might have been overlooked.

Since in birds deprived as adults the 2DG distribution shows no side difference, a sensitive period for the effects of monocular deprivation has to be assumed, as has been established for the mammalian visual system (e.g. Blakemore and Van Sluyters 1974). Results on two biochemical systems, the enzymes GAD and ChAT in the pigeon (Bagnoli et al. 1982), and the physiological findings of Pettigrew and Konishi (1976) on the owl's visual wulst also suggest the existence of an early sensitive period.

There is every reason to believe, that this critical period also exists for cell size changes. Measurements of rotundal cells of birds, whose eyes were not properly deprived because they lost their eyecaps for 1 or 2 days during the first 20 days of life (and were therefore omitted from this study), revealed no asymmetry in neuron size. We are currently investigating the time course of the sensitive period for the effects of monocular deprivation.

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