FUNCTIONAL POSTNATAL CHANGES IN AVIAN BRAIN REGIONS RESPONSIVE TO RETINAL SLIP: A 2-DEOXY-D-GLUCOSE STUDY¹

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Abstract

The postnatal development of two avian brain areas, the nucleus of the basal optic root (nBOR) and the lentiform nucleus of the mesencephalon (LM), was studied using the 2-deoxy-D-glucose (2-DG) method. Previous studies have shown that these nuclei respond to whole field visual motion, which is used for optokinetic eye movements.

In the present study vertical whole field visual motion presented to one eye resulted in the accumulation of 2-DG label in the contralateral nBOR in both hatchlings and 3-week or older chicks. In hatchlings the nBOR was diffusely labeled whether upward or downward motion was used as the test stimulus, whereas in older birds the label was localized within different subdivisions of the nBOR depending on the direction of vertical motion: upward motion resulted in concentration of 2-DG label in the dorsal nBOR, whereas downward motion resulted in label in the ventral nBOR.

Horizontal whole field visual motion presented to one eye resulted in 2-DG label in the contralateral LM and in the lateral portion of the contralateral nBOR in animals of both ages. In hatchlings, visual motion in both temporal-to-nasal and nasal-to-temporal directions resulted in labeling of both subdivisions of the LM, LM magnocellularis (LMmc) and LM parvocellularis. In older birds, temporal-to-nasal motion resulted in labeling of only the LMmc, whereas nasal-to-temporal motion produced labeling in both subdivisions.

These results strongly suggest that the nBOR and LM continue to develop their response properties postnatally and that different functional units become separated within particular subdivisions of the nuclei. Conceivably, the functional segregation within the nBOR is due to an intrinsic reorganization, whereas functional changes in the LM may be due to the postnatal development of a projection from the telencephalon.

Optokinetic nystagmus (OKN), the stabilizing eye movement induced by large field visual motion on the retina, has intriguing anatomical substrates. On the one hand, there is no doubt that there is subcortical circuitry adequate by itself to subserve the basic pattern of behavior, at least in non-primates. This includes the pretectum and the accessory optic system, and probably the vestibulocerebellum, pons, and vestibular nuclei as well. On the other hand, cortical processing of the retinal slip signal, i.e., large whole field visual motion on the retina, is clearly also important, both because the majority of relevant pretectal neurons receive cortical inputs (Schoppmann, 1981) and because, without cortical inputs, the behavior becomes asymmetric in that each eye responds more strongly in one horizontal direction than in the other (Wood et al., 1973; Hoffmann, 1981; Montarolo et al., 1981).

Since neonates of several species also display the same op-

tokinetic asymmetry (humans: Atkinson, 1979; Naegle and Held, 1982; monkeys: Atkinson, 1979; cats: Van Hof-Van Duin, 1976; Hoffmann, 1981, 1983), which disappears over the first few months, it has generally been assumed that this developmental change arises from changes in the cortical contribution. The subcortical organization has been regarded, plausibly enough, as fully functional at birth. We have studied differences in the postnatal development of two subcortical nuclei that respond to retinal slip signals.

In this study the 2-deoxy-D-glucose (2-DG) method (Sokoloff et al., 1977) was used to identify postnatal changes in labeling patterns in response to whole field visual motion in the chick accessory optic system and pretectum during the 3 weeks after hatching. In a nucleus of the accessory optic system the pattern of labeling in response to vertical motion changed from a diffuse labeling to a localized label in different subdivisions of the nucleus, depending on the direction of vertical motion. Since this nucleus receives its input primarily from the retina, we suggest that the functional parcellation of the nucleus is due to an intrinsic reorganization. In a nucleus of the pretectum the pattern of 2-DG labeling became restricted to specific portions of the nucleus depending on the direction of horizontal motion. This nucleus, like its homologue in mammals, is known to receive a telencephalic projection which may account for its postnatal development.

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Anatomical and Physiological Background

In mammals, birds, and amphibia it is generally agreed that non-horizontal retinal slip signals, i.e., vertical, torsional, or a combination of both, are transmitted to nuclei in the accessory optic system. In mammals these nuclei are the medial terminal nucleus, the dorsal terminal nucleus, and the lateral terminal nucleus. In birds, the nucleus of the basal optic root (nBOR; also known as the ectomammillary nucleus), which receives its principal projection directly from displaced retinal ganglion cells (Karten et al., 1977; Reiner et al., 1979; Fite et al., 1981), appears to respond most strongly to retinal slip which is either vertical or a combination of vertical and torsional (Burns and Wallman, 1981; Morgan and Frost, 1981). The predominantly vertical directional sensitivity of the nBOR has been confirmed by a metabolic mapping study (McKenna and Wallman, 1981a). The role of the nBOR in OKN has been suggested by the finding that electrolytic lesions in the nBOR result in an impairment of OKN to motion in vertical and torsional but not horizontal directions (Wallman et al., 1981).

The nBOR is located on the ventral surface of the mesencephalon, medial to the optic tectum. It consists of the nBOR proper, the nBOR pars dorsalis (nBORd), which forms a shell covering the nBOR on its dorsal and medial surfaces, and the nBOR pars lateralis (nBORl), which lies lateral to the nBOR over the optic tract and extends rostrally merging with the lentiform nucleus of the mesencephalon (chick: Fig. 1; pigeon: Brecha et al., 1980). The nBOR complex receives its afferents principally from the contralateral retina (Cowan et al., 1961; Repérant, 1973; Ehrlich and Mark, 1984); sparse projections from the ipsilateral retina (Repérant, 1973; O'Leary et al., 1983; M. D. Gottlieb and O. C. McKenna, unpublished observation),

contralateral nBOR (Brecha et al., 1980), and ipsilateral visual Wulst³ (Rio et al., 1983) have also been reported.

Horizontal retinal slip signals in birds appear to be transmitted to a pretectal nucleus, the lentiform nucleus of the mesencephalon (LM). This is suggested by a metabolic mapping study (McKenna and Wallman, 1981a), preliminary electrophysiological studies (Winterson and Brauth, 1981; Morgan et al., 1983), and a lesion study (Gioanni et al., 1983). These signals may be transmitted directly from the retina (Cowan et al., 1961; Repérant, 1973; Ehrlich and Mark, 1984) or indirectly from the visual Wulst (Karten et al., 1973; Miceli et al., 1979), or from the nBOR (Brecha et al., 1980). The metabolic mapping study also showed the nBORl to be responsive to horizontal retinal slip. In mammals the nucleus of the optic tract (NOT), a nucleus homologous to the LM (Kuhlenbeck, 1939), is also thought to process horizontal retinal slip signals and appears to be essential for horizontal OKN since electrical stimulation of the NOT produces horizontal nystagmus, whereas lesioning the nucleus eliminates horizontal OKN (Collewijn, 1975a, b).

In birds the LM is located in the pretectum rostral to the nBOR and just medial to the optic tectum. It consists of two subdivisions, the LM magnocellularis (LMmc), which is also known as the nucleus superficialis synencephali (Rendahl, 1924; Huber and Crosby, 1929), and the LM parvocellularis (LMpc) (Kuhlenbeck, 1939) (Fig. 2). The LMmc in its most rostral position lies just caudal to the optic tract and forms a thin continuous band of cells running dorsoventrally; more

³ The anatomical connections and electrophysiological properties of the visual Wulst in birds are extremely similar to those of the mammalian visual cortex (Karten et al., 1973; Fox, 1978; Pettigrew, 1978).

Figure 1. Photomicrograph of the nBOR complex seen medial to the optic tract (TrO) at the level of the infundibulum (INF) showing the nBORd (d), forming a cap around the nBOR proper (p), and the nBORl (l). The optic tectum (TeO) is seen dorsolaterally.

Figure 2. Photomicrograph of the LM and its subdivisions LMmc and LMpc. At this level the LM lies between the optic tectum (TeO) and the nucleus rotundus (NR). The LMmc (between dashed lines on the left) is found medial to the LMpc (between dashed lines on the right). TrO, optic tract.

caudally, the central portion of the nucleus disappears, leaving a small dorsal portion and a larger ventral portion; the latter extends caudally to the level of the nBOR where it appears to merge with the nBORl. This caudal portion of the LMmc has been termed the nucleus externus by a number of authors (Rendahl, 1924; Huber and Crosby, 1929; Repérant, 1973). The LMpc, as illustrated by Kuhlenbeck (1939), forms a continuous

band of cells running dorsoventrally in the rostral pretectum and lying lateral to the LMmc. The LMpc can be further subdivided into medial and lateral portions on the basis of cell density and orientation of fibers (Ehrlich and Mark, 1984). All portions of the LMmc and LMpc receive direct retinal projections, although the density of terminals in the LMmc is much greater (Ehrlich and Mark, 1984; M. D. Gottlieb and O. C. McKenna, unpublished observation).

Materials and Methods

Subjects and apparatus. The subjects were White Leghorn chicks (*Gallus gallus domesticus*) of two different ages—2 to 8 days and 3 to 5 weeks—referred to here as “hatchlings” or “older chicks,” respectively. The use of chicks in 2-DG studies of the visual system has the advantage that their optic nerves are almost entirely crossed. Therefore, each eye can view a different visual stimulus, and the level of radioactivity produced by the accumulation of 2-DG and its principal metabolite, 2-deoxy-D-glucose-6-phosphate, can be compared in the same structure on both sides of the same transverse or horizontal brain section. As a consequence, technical problems such as variation in the 2-DG dose, film exposure times, and film developing procedures, which make comparisons between animals difficult, are eliminated, and paired data analysis can be used to evaluate densitometric readings of the equivalent structures on both sides of the brain.

For exposure to visual motion, animals were placed, with their heads restrained, in a container suspended in an evenly lit, striped optokinetic drum that was rotating either about a vertical or a horizontal axis at 2 to 4°/sec. (See preceding paper (Wallman and Velez, 1985); for a detailed description of the experimental apparatus.) This stimulus velocity was selected since single-unit recordings in the nBOR have shown that units respond best to low velocities (Burns and Wallman, 1981). Since the birds presumably showed OKN during the stimulus presentation and since the instantaneous eye velocity is quite variable, especially during stimulation in non-horizontal directions, our stimulus situation resulted in the eye viewing a broad range of low stimulus velocities. In control experiments a higher velocity (100°/sec) was used.

Experimental manipulations. In experiments using whole field vertical motion, animals were tested either monocularly or binocularly. Under monocular test conditions the experimental eye viewed either upward or downward motion,⁴ whereas the control eye either was covered with a translucent occluder or viewed stationary stripes oriented vertically. (The use of stationary stripes assured that the same contours were seen by each eye. The use of vertical stripes for the control eye assured that vertical OKN of the control eye stimulated by the visual motion seen by the experimental eye would result in minimal movement of contours on the retina.) The response to either control situation was similar. Six hatchlings were tested in this manner. Of the older birds, four were tested monocularly with one eye viewing upward motion (two birds) or one eye viewing downward motion (two birds) and the other eye covered by a translucent occluder. In addition, three older animals were tested binocularly with each eye viewing vertical motion in a different direction. In these cases, the animals were oriented in the drum so that one eye viewed upward linear motion and the other eye viewed downward and clockwise cyclorotation. These directions approximated the two directions upward and a combination of downward and anterior, shown to produce maximal single-unit activity in the nBOR (Burns and Wallman, 1981). In these experiments five animals viewed each direction of vertical motion.

In experiments using whole field horizontal movement as the visual stimulus, the animals were tested either monocularly, with one eye covered with a translucent occluder and the other eye left uncovered viewing either temporal-to-nasal motion (three hatchlings, three older chicks) or nasal-to-temporal motion (three hatchlings, three older chicks), or binocularly, with both eyes uncovered so that one viewed nasal-to-temporal movement and the other viewed temporal-to-nasal movement of the drum (four hatchlings, six older chicks). In a separate group of experiments the medial and lateral recti of the eyes of four older chicks were cut 1 to 2 days before binocular testing in an attempt to reduce the effects of eye movements on the retinal slip on each eye. To verify that the eye muscles had been transected, the eye muscles

⁴ As in the preceding paper (Wallman and Velez, 1985), we identify motion directions as those seen looking along the optic axis of the eye.

were dissected after removal of the brain for the 2-DG experiments. In addition, three older chicks were tested binocularly at a drum velocity of 100°/sec.

2-DG method. All animals were injected intracardially or intravenously with [¹⁴C]-2-deoxy-D-glucose (0.16 μ Ci/gm; specific activity, 300 to 350 mCi/mM; Amersham) and placed immediately in the optokinetic drum for 45 min, after which animals were removed and injected with an overdose of urethane. Brains either were not fixed or were fixed for 5 to 10 min by an intracardial perfusion with 4% buffered formalin; after dissection, brains were quickly frozen in isopentane cooled by liquid nitrogen and cut in the transverse, horizontal, or sagittal plane at 20 μ m in a cryostat. Sections were picked up on warm coverslips, dried quickly on a slide warmer at 70 to 90°C, and placed against either Kodak SB 5 x-ray film for 6 days, DuPont Lo-dose x-ray film for 13 days, or Kodak Electron Image film for 5 to 6 weeks. The same sections used for autoradiography were later stained with cresyl violet or thionin and then photographed. In order to identify the nuclei and their subdivisions that had accumulated label, the autoradiographs were projected onto the photographs of their matching stained sections using an Aus Jena projector, and the areas displaying label were drawn on clear acetate sheets attached to the photographs.

The use of the 2-DG method has the powerful advantage of showing the spatial distribution of neural activities over large areas of the brain in individual animals. The method suffers, however, from the inability to distinguish cellular activity from terminal activity and excitatory from inhibitory activity. The most important caveat regarding the use of this method in this study is that, since the animals' eyes were not immobilized, stimulus velocity on the retina was not controlled. As pointed out above, during the slow phase of OKN the eye velocity and hence the retinal slip velocity varies. A second caveat, relevant to the binocular exposure experiments, is that OKN in chicks is not strictly conjugate, resulting in different retinal slip velocities on each eye. As reported below, we found that, when the eye muscles were cut or when the drum velocity was sufficiently fast to equalize the retinal slip velocities on both eyes, differences in the density of labeling of the two LMs became apparent. Another consequence of binocular testing was that labeling not detected during monocular testing became apparent, suggesting that weak activity in the ipsilateral nuclei was not detectable with this method without the additional metabolic activity provided by the contralateral projections.

Densitometric analysis. To quantify differences in optical density of the autoradiograms of nuclei on two sides of the brain, the image of the autoradiogram was projected onto the drawing of the relevant nucleus, as just described, and the light intensity at three different points within the nucleus was measured and averaged. Readings from the autoradiograms of the LM and nBORl on each side of the brain were made in 3 to 10 sections/brain after binocular testing with horizontal motion from three hatchlings, three older animals, and three older animals whose horizontal eye muscles had been transected. In hatchlings tested with one eye viewing vertical motion and the other viewing stationary stripes, densitometric readings of both nBORs were made in 5 to 19 sections/brain. This resulted in paired data that were expressed as ratios and analyzed statistically using the Student's *t* test.

Since in older birds the position of 2-DG label was concentrated within particular portions of the nBOR, depending on the direction of vertical motion, a method to analyze the dorsoventral position of the label was devised. A transverse brain section at the level of the caudal infundibulum, approximately at the center of the rostrocaudal extent of the nucleus, was selected, and the image of the nBOR was projected and drawn on polar coordinate graph paper which was then used as a template for the autoradiograms. From the arc of the circle that best fit the dorsal surface of the nBORd, three radial lines converging ventral to the surface of the brain were drawn, so that the nucleus was divided into four approximately equal portions. Autoradiograms were superimposed on the template and four readings were made equidistant along each radial line with the most dorsal and most ventral points being near the boundaries of the nBOR. The most dorsal reading on each radial line fell within the nBORd (division 1 in Fig. 8), whereas the other three readings fell within the nBOR proper (divisions 2, 3, and 4 in Fig. 8). To analyze the dorsoventral differences quantitatively, we determined the maximum density along each dorsoventral measurement track of the autoradiograms. This ranking method has the advantage of being immune to mediolateral and anteroposterior differences in uptake or background and in not being dependent on an assessment of the radioactivity-optical density function. Although this method has

the disadvantage of presenting ranks rather than raw data, the advantage of having each section with equal weight in the results outweighs the disadvantage and gives a conservative estimate of the changes present. Since there are three measurement tracks/section and 4 sections/animal, each animal contributes 12 points. Sections from 15 brains were analyzed in this manner.

Results

Vertical retinal slip stimulation

Hatchlings

Monocular testing. When hatchlings were tested with one eye viewing slow vertical motion, either upward or downward, and the other eye viewing stationary stripes, the nBOR contralateral to the eye viewing motion appeared more heavily labeled than the ipsilateral nBOR (Figs. 3 and 4). This observation was verified by measurements of the light transmission in the autoradiograms of the nBOR proper on both sides of the brain; statistical analysis of readings in 5 to 19 sections from three animals showed that the ratios of the light transmission of the ipsilateral (unstimulated) to the contralateral (stimulated) nBOR were significantly different from 1 (Student's *t* test, Table 1). Neither nBORl nor the LM in the hatchlings displayed detectable 2-DG labeling after testing with vertical motion. Hatchlings were not tested under binocular conditions.

Older birds

Monocular testing. In older birds, vertical motion also resulted in the appearance of 2-DG label in the contralateral nBOR. Unlike the hatchlings, however, localization within specific subdivisions of the nBOR was dependent on the direction of vertical motion. Figures 5 and 6 show the position of the label within the nBOR in a series of autoradiograms and in a stained section from which one of the illustrated autoradiograms was made. Stimulation with upward visual motion resulted in labeling of the nBORd and, in some cases, of the dorsal portion of the nBOR proper (Fig. 5). When autoradiograms and sections were studied throughout the rostrocaudal extent of the nucleus, the label was consistently localized in or adjacent to the nBORd throughout the middle third of the nucleus. In the rostral third, localization of the label in the nBOR varied; in two brains the label was clearly concentrated in the nBORd, whereas in the other three brains the entire nucleus at this level appeared diffusely labeled. In the caudal third of the nBOR, the label either was light and uniformly distributed in the nBORd and nBOR proper (two of five brains) or was not detectable (three of five brains). In contrast, viewing downward or downward and cyclorotational motion resulted in the concentration of the label in the central nBOR proper, sparing the nBORd and in most cases the most ventral portion of the nBOR proper (Fig. 6); this location of the label was seen throughout the rostrocaudal extent of the nucleus.

Binocular testing. The differential labeling of the nBOR was also seen in autoradiograms of brains from animals tested with both eyes open, one viewing upward motion and the other viewing downward and cyclorotational motion (Fig. 7). The distribution of the label in the nBOR was similar to that seen in animals tested monocularly. Consequently, the data from animals from both test situations were combined for the following analysis.

Detailed densitometric analysis of distribution of label within nBOR

Since the position of the 2-DG label appeared to shift within the nBOR subdivisions with age, a more detailed analysis of the position of label within the nBORd and nBOR proper was made (see "Materials and Methods" and Fig. 8). In hatchlings

Figures 3 and 4. Autoradiograms and matched stained brain sections from hatchlings viewing either upward (Fig. 3) or downward (Fig. 4) motion with one eye and stationary stripes with the other. Figures 3A and 4A are autoradiograms showing that the label in the nBOR (arrow) contralateral to the eye viewing vertical motion is denser. Figures 3B and 4B are the matched stained sections showing that label in the autoradiograms, a higher magnification of which is seen in the inset, is present in the nBOR (dashed lines). The infundibulum is indicated (INF).

TABLE I
2-DG labeling of nBOR in hatchlings tested with vertical motion

	Light Transmission Ratio ^a	Probability
Bird 1	0.84 ± 0.06 ^b (8) ^c	$p < 0.05$
Bird 2	0.88 ± 0.04 (19)	$p < 0.005$
Bird 3	0.85 ± 0.05 (5)	$p < 0.01$

^a Ratios of the percentage of light transmission of nBOR on the right and left sides of brain sections.

^b Values are the means ± SE.

^c Numbers in parentheses, number of sections measured.

viewing upward motion, the position of maximum 2-DG label was found throughout the nBOR proper and the nBORd, whereas the locus of maximum label in animals viewing downward motion was dispersed within the nBOR proper with little labeling in the nBORd (Fig. 8). The two stimulus directions did not produce significantly different results ($\chi^2 = 5.6$, $p > 0.05$ with all categories used), although there was a tendency like that found in the older animals, as described below. We cannot say whether the differences in labeling distribution within the nucleus with upward or downward motion are present at hatching, since our "hatchlings" were 2 to 8 days old at testing. In the older birds tested with upward visual motion, the position of maximum 2-DG label was generally found in the most dorsal position of the nBOR sampled (position 1 in Fig. 8) and to some extent in the position just ventral to it (position 2), whereas, when tested with downward visual motion, the position of maximum label was concentrated in positions 2 and 3, a statistically highly significant difference ($\chi^2 = 55.3$, $df = 2$, $p < 0.001$, positions 3 and 4 combined). When results from the hatchlings and older birds that had been tested with each stimulus direction were compared, they were found to be statistically different (upward: $\chi^2 = 39.3$, $df = 2$, $p < 0.001$;

downward: $\chi^2 = 11.5$, $p < 0.01$). The very low level of labeling found in position 4 in older birds as opposed to the hatchlings might be explained by the progressive myelination of axons that lie along the ventral surface of the nucleus (O. C. McKenna and M. D. Gottlieb, unpublished observation) and compose a portion of the basal optic root which innervates the nBOR.

Other observations

As an additional test of whether the 2-DG labeling corresponds to known neuronal characteristics, we tested animals with whole field vertical motion at a high velocity (100°/sec) which results in retinal slip velocities of approximately 90°/sec (Wallman and Velez, 1985). We expected that this manipulation would result in reduced 2-DG uptake since the neurons in the nBOR are not responsive to retinal slip velocities above 40°/sec (Burns and Wallman, 1981). In three older animals tested with upward or downward motion, little or no labeling of any portion of the nBOR was seen although the LM and outer layers of the optic tectum acquired very dense label. The LM is known to contain high-velocity-sensitive units (B. J. Winterson and S. E. Brauth, submitted for publication).

In the older animals exposed to either direction of vertical motion, the contralateral LM became lightly labeled. However, unlike the nBOR, the position of the label in the LM did not vary with the direction of vertical motion.

Horizontal retinal slip stimulation

Hatchlings

Monocular testing. When hatchlings were tested with one eye viewing temporal-to-nasal motion and the other eye covered by a translucent occluder, both divisions of the LM and the nBORl contralateral to the eye viewing motion were labeled, whereas the ipsilateral LM or nBORl did not exhibit detectable label. When nasal-to-temporal motion was used as the test stimulus,

Figures 5 and 6. Autoradiograms (A to D) and matched stained sections (A') from older chicks viewing vertical motion. **Figure 5.** A to D, Autoradiograms of brain sections of a 5-week-old bird showing the nBOR (arrows) contralateral to the eye viewing upward motion. Figure 5A' is the stained section from which autoradiogram 5A was made showing the position of dense label (dashed lines) over dorsomedial nBOR. The inset is a higher magnification of label seen in Figure 5A. **Figure 6.** A to D, Autoradiograms of brain sections at the level of the nBOR (arrows) of a 4-week-old bird. The eye contralateral to the labeled nBOR viewed downward motion. The inset is a higher magnification of the label in autoradiogram 6A. Figure 6A' is the stained section from which autoradiogram 6A was made showing the position of dense label (dashed lines) over nBOR proper. The bubble shown in the inset (arrow) and in the stained section (arrow) lies in nBORd which is not labeled.

fainter labeling was seen again in the contralateral LM; the distribution of label in the LM was similar to that seen when the opposite direction was used as the visual stimulus. Since we never detected label in the ipsilateral LM and nBORl, densitometric readings were not made. The distribution of the label within the LM and nBORl under both test conditions resembled that seen in Figure 9.

Binocular testing. When hatchlings were tested binocularly, both divisions of the LM (Fig. 9, B' and B'') and nBORl (Fig. 9, F' and F'') contralateral to the eye viewing temporal-to-nasal motion displayed heavy labeling, whereas the LM and nBORl contralateral to the eye viewing nasal-to-temporal motion displayed little or no label (Fig. 9). Statistical analysis of densitometric readings of the LM and nBORl on both sides of the brain in three to six sections from three animals demon-

strated that the ratios of the light transmission were significantly different from 1 (Student's *t* test, Table II). The LM was traced in autoradiograms as the nucleus extended caudally through the pretectum to the level of the nBOR complex where it merged with the labeled nBORl (Fig. 9, A to F). The exact position of the merger of these structures could not be determined in our specimens since the size and shape of the cells in each nucleus, as seen in the cryostat sections, are similar.

Older birds

Monocular testing. In older birds, the LM and nBORl also became labeled in response to both directions of horizontal motion, but localization of the label within the LM depended on the direction of motion presented. When tested with the uncovered eye viewing temporal-to-nasal motion, the contra-

Figure 7. Autoradiogram and matched stained section from a 3½-week-old bird with each eye viewing motion in a different vertical direction. In A the labeled structure on the left is contralateral to the eye viewing upward motion (arrow); the labeled structure on the right is contralateral to the eye viewing downward motion (arrow). B, Stained section of the left nBOR showing the position of the label in the nBORd (dashed lines) seen in A. C, Stained section of the right nBOR showing the position of the label in the nBOR proper (dashed lines) seen in A. The positions of the meninges (M) seen in the autoradiogram are apparent in the stained sections.

lateral LMmc but not the LMpc became labeled in four of five birds (Fig. 10). When tested with nasal-to-temporal motion, label was found in both subdivisions of the contralateral LM in six of six brains (Fig. 11). As in the hatchlings, label was never seen in the ipsilateral LM or the nBORl regardless of the directions of stimulus motion, suggesting that retinal slip information reaches the LM primarily from the contralateral eye. Curiously, the 2-DG labeling in the LMpc did not cover the entire subdivision but instead appeared as a diagonal band running dorsolaterally to ventromedially, where it appeared to meet the label in the LMmc. The nBORl contralateral to the eye viewing either direction of horizontal motion also displayed label.

Binocular testing. When birds were tested with both eyes uncovered so that one eye viewed temporal-to-nasal motion and the other eye viewed nasal-to-temporal motion, the LMmc and the medial portion of the LMpc became labeled on both sides of the brain (Fig. 12). This finding is not predictable from the results under monocular exposure conditions. Since only the contralateral LMmc became labeled under monocular conditions, it appears that stimulation of the ipsilateral eye with nasal-to-temporal motion is responsible for the additional labeling of the LMpc.

In addition, during binocular testing, the density of label in the LM and nBORl on both sides of the brain did not show a consistent difference (Table II); the LM and nBORl contralateral to the eye viewing temporal-to-nasal motion were not significantly different from the ipsilateral nuclei in two of three birds. This result was surprising since older birds have a higher OKN gain (eye velocity/stimulus velocity) to stimuli moving in the temporal-to-nasal direction (Gioanni et al., 1981; Wallman and Velez, 1985) and lesions of the LM preferentially eliminate OKN in this direction (Gioanni et al., 1983). These apparently opposing results may be reconciled by considering that the better the OKN is in a particular direction, the less retinal slip would be experienced in that direction, perhaps resulting in less metabolic activity in the contralateral LM. This would account for our results since, during binocular OKN, the retinal slip velocity seen by each eye differs because in birds the eyes are only partially yoked; the eye viewing temporal-to-nasal motion has higher OKN gain than the eye viewing nasal-to-temporal motion, resulting in a lower retinal slip velocity in the eye viewing temporal-to-nasal motion and in the LM contralateral to that eye. Thus, in directions in which the optokinetic gain was high, the retinal slip velocity would be low and the nuclei studied here might show a weaker response to what

Figure 8. Histograms of points with the maximum density along each dorsoventral track shown in the drawing (inset), in hatchlings and 3- to 5-week-old chicks tested with either upward or downward motion. The results are described in the text. Arrows indicate the means.

is, in fact, the direction to which they respond most strongly. To test this possibility, experiments were designed to reduce the difference in the retinal slip velocities between the two eyes by either cutting the medial and lateral recti muscles and testing the animals at 2 to 4°/sec or testing animals at 100°/sec, a velocity at which the retinal slip velocities in both eyes are approximately equal, with all eye muscles intact. When three birds were tested binocularly after transection of eye muscles, the labeling that was seen in the LM contralateral to the eye viewing temporal-to-nasal motion was heavier than that of the ipsilateral LM in all three animals; the density of labeling in the contralateral nBORl of two of these animals was also greater. Densitometric readings confirmed these observations (Table III). When four animals were tested at the high velocity of motion, a similar difference in labeling in the LM and the nBORl was seen (Fig. 13). Under either test condition the distribution of label within the LM was similar to that seen in the initial experiments. These results suggest that when both eyes are viewing the stimulus at approximately the same velocity, greater metabolic activity is found in the LM and nBORl contralateral to the eye viewing temporal-to-nasal motion.

Other nuclei displaying 2-DG labeling

We observed no nuclei other than the nBOR and LM that became labeled differentially on the two sides of the brain during these experiments. Several nuclei, however, became labeled on both sides of the brain; these were: the nucleus rotundus, the pretectal nuclei, the visual Wulst, the oculomotor complex, the nucleus ovoides (Figs. 9, 12, and 13), and nucleus mesencephalicus lateralis, pars dorsalis (Fig. 9) of the auditory system and all of the vestibular nuclei, especially the nucleus vestibularis medialis.

Discussion

Relation to electrophysiological and optokinetic behavior studies

This metabolic mapping study shows that two sensory nuclei that respond to retinal slip signals, the nBOR and LM, are not fully developed at hatching but continue to develop during the first few weeks of postnatal life.

nBOR. The postnatal changes in the nBOR result in the functional parcellation of the nucleus. In hatchlings, upward motion results in an even distribution of 2-DG label throughout both the nBORd and nBOR proper, whereas the same visual stimulus in older birds results in a concentration of label principally in the nBORd but also in the adjacent portion of the nBOR proper. Downward motion in hatchlings produces a diffuse labeling of the entire nBOR proper, whereas, in older chicks, it produces a concentration of label in the center of the nBOR proper; the nBORd is unresponsive to downward motion at either age. Corroboration of these findings has been provided by electrophysiological and optokinetic behavior studies. In hatchlings, single units responsive to upward motion have been recorded intermingled with units responsive to downward motion within the nBOR proper (S. Burns, personal communication); in contrast, in older chicks upward responsive units are localized in the nBORd and the adjacent nBOR proper, whereas downward responsive units are found only ventral to these regions in the nBOR proper (Burns and Wallman, 1981). The postnatal reorganization of the nBOR may also be reflected in the postnatal shift that occurs in optokinetic behavior postnatally. As shown in the preceding paper (Wallman and Velez, 1985), when stimulated by non-horizontal visual motion, hatchlings perform OKN best when the visual stimulus is moving in an upward and torsional direction, whereas older birds respond best to motion that is in a downward and torsional direction.

Although in the older birds the nBORd acquires label only in response to upward motion, the region of upward responsiveness does not follow the nBORd boundaries. In the rostral third of the nucleus after stimulation with upward motion, 2-DG label is seen spread throughout the nBOR proper and nBORd in three of five brains studied. In contrast, in the middle third of the nucleus the label is found only in that part of the nBOR proper adjacent to the nBORd as well as in the nBORd. A similar distribution of up responsive units within the rostral nBOR has been demonstrated using single-unit recordings (S. Burns, personal communication).

LM. The response properties of the LM also change postnatally. First, in older birds the temporal-to-nasal motion no longer produces 2-DG uptake in both subdivisions of the LM

Figure 9. Autoradiograms and photomicrographs of stained sections from the brain of a hatchling that viewed horizontal motion with both eyes open. *A* to *F*, Autoradiograms show labeling on the *right* (arrow) contralateral to the eye viewing temporal-to-nasal motion, whereas equivalent structures on the *left*, contralateral to the eye viewing nasal-to-temporal motion, show little or no label. Higher magnifications of autoradiogram *B* and of the stained section from which it was made are seen in *B'* and *B''*. Dashed lines in *B''* show the position of label in LM. Comparison to Figure 2 indicates that the label is present both in the LMmc and LMpc. Higher magnifications of autoradiogram *F* and of the stained section from which it was made are seen in *F'* and *F''*. Dashed lines in *F''* show the position of label in nBORl. The heavily labeled bilateral structure seen in autoradiograms *A* to *D* is nucleus ovoideus (OV) and that in autoradiogram *F* is nucleus mesencephalicus lateralis (ML). NR, nucleus rotundus; TeO, optic tectum.

but only in the LMmc. This shift in directional sensitivities has not yet been confirmed by single unit recordings, but a concentration of low velocity responsive units in the LMmc of adult pigeons has recently been reported (Winterson and Brauth, 1984). Second, the LM in older birds is responsive not only to horizontal but also to vertical directions of motion; this has been confirmed by electrophysiological studies (Winterson and Brauth, 1981; B. J. Winterson and S. E. Brauth, submitted for publication).

Our finding that, in hatchlings, the LM contralateral to the eye viewing nasal-to-temporal motion acquires 2-DG label during monocular but not binocular stimulation can be explained by differences in the eye velocity and, hence, the retinal slip velocity, under the two test conditions. Under binocular test

conditions OKN would be substantially better in the eye seeing nasal-to-temporal motion than it would under monocular conditions (Gioanni et al., 1981; J. Wallman and J. Velez, personal communication); consequently, the retinal slip signal to the LM would be less, resulting in less 2-DG uptake. The hypothesis that 2-DG labeling requires a minimal amount of retinal slip is indirectly supported by preliminary results showing that, under binocular conditions, nasal-to-temporal stimulation can result in labeling in LM if the eyes are immobilized, thereby assuring substantial retinal slip.

Developmental mechanisms responsible for postnatal changes in the nBOR and LM

Both the nBOR and LM continue to develop postnatally; the mechanism of the postnatal changes may differ since the nBOR

TABLE II
2-DG labeling of LM and nBORl after binocular horizontal testing

	Lentiform Nucleus ^a		nBORl ^a	
	<i>Hatchlings</i>			
Bird 4	0.77 ± 0.03 ^b	(4) ^c $p < 0.005$	0.68 ± 0.05	(6) $p < 0.005$
Bird 5	0.78 ± 0.07	(5) $p < 0.005$	0.83 ± 0.01	(3) $p < 0.005$
Bird 6	0.76 ± 0.06	(4) $p < 0.05$	0.71 ± 0.09	(3) $p < 0.005$
	<i>3- to 5-Week Chicks</i>			
Bird 7	0.73 ± 0.03	(10) $p > 0.005$	0.72 ± 0.06	(4) $p < 0.005$
Bird 8	1.03 ± 0.04	(6) $p > 0.1$	1.14 ± 0.05	(4) $p < 0.05$
Bird 9	0.82 ± 0.13	(4) $p > 0.1$	1.94 ± 0.63	(3) $p > 0.1$

^a Ratios of the percentage of light transmission of structures on the right and left side of brain sections.

^b Values are the means ± SE.

^c Numbers in parentheses, number of sections analyzed.

receives its input primarily from the retina, whereas the LM receives a strong "cortical" input from the visual Wulst as well as a projection from the retina. These anatomical arrangements as well as the single-unit recording data on the nBOR suggest that developmental changes in the nBOR may be intrinsic to the nucleus, whereas those in the LM may be influenced by a projection from the telencephalon.

nBOR. The developmental changes that occur in the nBOR might be explained by a number of mechanisms. The first and most probable possibility is that retinal ganglion cell terminal arbors conveying different types of retinal slip signals redistribute to the subdivisions of the nBOR. This redistribution could

occur either by pruning back of axon terminals or by the growth of dendrites and their synaptic connections into different subdivisions of the nBOR. In the first case, in hatchlings, retinal axon terminals transmitting upward retinal slip signals would terminate on neurons in both subdivisions; during the first few postnatal weeks those terminals to the nBORd and adjacent nBOR proper would remain, whereas those to the ventral nBOR proper would be lost. In the second case, rather than losing the afferents to the ventral nBOR, dendrites of neurons in the nBOR proper would be growing toward the nBORd carrying their axon terminals along with them. In either case, this shift in the position of the axodendritic synapses would be seen as a shift in the 2-DG labeling pattern if axon terminals in the nBOR accumulate 2-DG in preference to cell bodies (Mata et al., 1980; Sokoloff, 1981; Hökfelt et al., 1983). Terminals carrying downward retinal slip signals apparently do not terminate in the nBORd in the hatchling (see Fig. 8), suggesting that the only postnatal change may be a modest shifting of terminals and/or cells dorsally into the center of the nBOR proper. Postnatal remodeling of axon terminals resulting in a segregation of inputs has been demonstrated in a number of brain areas: for example, development of ocular dominance columns (Hubel et al., 1977; LeVay et al., 1978), reduction in climbing fiber input to cerebellar Purkinje cells (Crepel et al., 1976; Mariana and Changeux, 1981), and reduction in corpus callosal projections (Innocenti and Caminiti, 1980; O'Leary et al., 1981). The suggestion from our results, that synaptic contacts are continuing to develop and mature during the first 3 weeks of postnatal life, is supported by the finding in the hatchling

Figures 10 and 11. Autoradiograms and stained sections from brains of older birds tested monocularly with temporal-to-nasal (Fig. 10) or nasal-to-temporal (Fig. 11) motion viewed by the contralateral eye. Figure 10. Arrows indicate the label in A to C. Figure 10C' is the matching stained section of autoradiogram C and shows the position of the label (dashed lines) in LMmc. Figure 11. Single arrows indicate the LMmc and double arrows indicate the LMpc in autoradiograms A to C. Figure 11C' is the matching section to autoradiogram C and shows the position of the label (dashed lines) in the LMmc and in a diagonal band in the LMpc. NR, nucleus rotundus; TeO, optic tectum.

Figures 12 and 13. Autoradiograms from brains of older birds tested binocularly with horizontal motion at slow (2 to 4°/sec, Fig. 12) or fast (100°/sec, Fig. 13) velocity. The heavily labeled bilateral structure seen medially (Figs. 12, A and B, and 13, A and B) is the nucleus ovoides (OV). Figure 12. At slow velocity the label (arrows) appears symmetrical in the LM (A and B) and the nBORl (C). Figure 13. At high velocity the label is heavier in the LM (A and B) and nBORl (C, arrows) that are contralateral to the eye viewing temporal-to-nasal motion (arrows). Bilaterally symmetrical label is also seen in the outer layers of the optic tectum (TO). In Figures 12 and 13, A and B, right and left halves of different sections have been matched since the brain was not cut in a true transverse plane.

TABLE III

2-DG labeling of LM and nBORl after transection of horizontal eye muscles

	Lentiform Nucleus	nBORl
Bird 10	0.86 ± 0.06 ^b (6) $p < 0.05$	0.88 ± 0.04 (5) $p < 0.05$
Bird 11	0.84 ± 0.03 (6) $p < 0.01$	0.92 ± 0.01 (4) $p < 0.01$
Bird 12	0.85 ± 0.04 (5) $p < 0.05$	1.03 ± 0.04 (5) $p > 0.05$

^a Ratios of the percentage of light transmission of structures on the right and left sides of brain sections, after testing binocularly with horizontal motion.

^b Values are the means ± SE.

^c Numbers in parentheses, number of sections analyzed.

nBOR that some single units are broadly directionally tuned whereas single units in older birds are narrowly tuned to specific directions (Burns and Wallman, 1981, 1982).

A second possible mechanism would be the migration of neurons, which have already formed their appropriate synaptic connections, from one subdivision of the nBOR to another carrying axon terminals with them. Consequently, neurons responsive to upward movement would migrate from the nBOR proper into or adjacent to the nBORd, whereas cells responsive to downward movement would migrate from the most ventral portion of the nBOR proper to its central and dorsal portions. Whereas most developmental studies report that cellular migrations are complete prior to the formation of synaptic contacts, a few axosomatic synapses have been reported on migrating motoneurons in the early developing amphibian spinal cord (Chu-Wang et al., 1981; Liuzzi et al., 1983). It appears unlikely that the equivalent situation would occur in the postnatal nBOR, first, because at this stage of development the nBOR is almost fully developed in terms of its size and shape and, second, because its neurons are probably contacted by many functional axon terminals, as suggested by the large receptive fields of nBOR neurons in the hatchling (S. Burns, personal communication), making it unlikely that the neurons migrate within the nucleus dragging their afferents behind them.

Finally, it is possible that those displaced retinal ganglion cells (DRGCs) which develop postnatally might make more spatially ordered connections in the nBOR. This mechanism is suggested by a retrograde horseradish peroxidase (HRP) transport study showing that the number of HRP-labeled DRGCs almost doubles between the age of 2 days and 3 weeks (Reiner et al., 1979). Although this increase in the number of labeled cells may simply reflect a maturation of the cells' ability to

transport HRP retrogradely, if additional DRGCs do in fact develop postnatally and if their axons grow into the nBOR, those conveying upward motion retinal slip signals might be directed into the nBORd, and those conveying downward retinal slip signals might be directed into the nBOR proper.

LM. Several changes in the metabolic responsiveness of the LM occur postnatally. First, the LM becomes responsive to vertical as well as horizontal motion. These vertically directed retinal slip signals might reach the LM indirectly via a projection from the ipsilateral nBOR (Brecha et al., 1980), which might grow into the LM during the first 3 postnatal weeks. Second, in response to temporal-to-nasal motion presented monocularly, the 2-DG label is restricted to the LMmc in older chicks, whereas in hatchlings the label is found in the LMpc as well. This suggests the possibility that axon terminals responsive to temporal-to-nasal motion are being pruned back during the first few weeks of life or that neurons in the LMpc receiving temporal-to-nasal slip information may migrate into the LMmc. Third, during normal OKN of unrestrained eyes, the LM labeling becomes more symmetric with age, although this symmetry is not seen if the eye is immobilized. One could argue that the symmetry in the older birds is simply a result of greater activity being provoked by the greater retinal slip in the nasal-to-temporal direction due to a weaker OKN response in that direction in older birds, but it remains an open question whether these developmental changes in symmetry of labeling are simply a function of the different retinal slips present. The fact that the OKN behavior becomes strikingly more asymmetric as the 2-DG label becomes more symmetric at least argues for caution in extrapolation from metabolic patterns to behavioral output. Fourth, in older birds, the distribution of the label in response to nasal-to-temporal motion changes from a diffuse labeling of the LMpc to a distinct diagonal band within the LMpc. Conceivably, this developmental change may be due to the postnatal development of a projection from the visual Wulst which may also affect the directional asymmetry of the OKN. We base this suggestion on strong evidence in cats that the cortico-pretectal pathway provides nasal-to-temporal retinal slip signals to the NOT (Wood et al., 1973; Harris et al., 1980; Hoffmann, 1981; Montarolo et al., 1981) and develops postnatally (Van Hof-Van Duin, 1976; Hoffmann, 1981, 1983). If, in chicks, an equivalent projection from the visual Wulst grows into the LM postnatally, the question arises about the function of this projection. Since the appearance of the diagonal labeling pattern in the LMpc coincides with the reduction in OKN response in the nasal-to-temporal direction in older chicks, it may be that the reduction is due to the inhibition of nasal-to-

temporal responsive units in the LM caused by the newly active afferents from the Wulst.

The mechanisms responsible for the postnatal reorganization of the LM and nBOR are not known. The occurrence of the remodeling of these nuclei after hatching suggests the possibility that visual experience may play a role in their development. Preliminary experiments show that chicks deprived of form vision from hatching do not develop adult 2-DG labeling patterns in the nBOR when tested with vertical retinal slip stimulation but, instead, display 2-DG labeling patterns typical of hatchlings (McKenna et al., 1983).

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