level units, corresponding to 5.5 fmole of spiroperidol per milligram of protein. In contrast, the mean difference between lesioned and nonlesioned sides in the animals with grafts that reduced rotation was only 0.7 ± 1.7 gray level units (0.42 fmole per milligram). The difference between reduced and nonreduced rotation groups was statistically significant [$T(22) = 2.88, P < 0.01$] (Fig. 2).

The degree of denervation supersensitivity measured here by [^{3}H]spiroperidol autoradiography in slices was fairly well correlated with the results of previous studies in vitro. Several investigators (*15*) have found a 15 to 45 percent increase in receptor density in whole striatal homogenates after dopamine denervations. Further research is necessary to determine whether the characteristics of in vitro radioligand binding differ for dorsomedial and lateral striatal dopamine receptors.

In conclusion, the ameliorating effect of grafts of fetal substantia nigra on lesions of the nigrostriatal dopamine system is specific and is not produced by grafts of other parts of the fetal brain. The reductions in drug-induced rotation are associated with reductions in receptor sensitivity in graft recipients. Thus, grafts of fetal substantia nigra may release dopamine not only when stimulated by amphetamine but also spontaneously on a tonic basis. This produces an adjustment of the functional status of dopaminergic receptors in nearby areas, causing them to return to a more normal level and diminishing the apomorphine-induced behavioral response.

WILLIAM J. FREED
GRANT N. KO
Preclinical Neurosciences Section,
Adult Psychiatry Branch,
National Institute of Mental Health,
St. Elizabeths Hospital,
Washington, D.C. 20032
DEBRA L. NIEHOFF
MICHAEL J. KUHAR
Department of Neuroscience,
Johns Hopkins University School of
Medicine, Baltimore, Maryland 21205
BARRY J. HOFFER
Department of Pharmacology,
University of Colorado Health
Sciences Center, Denver 80262
LARS OLSON
Department of Histology, Karolinska
Institute, Stockholm, Sweden
H. ELEANOR CANNON-SPOOR
JOHN M. MORIHISA
RICHARD JED WYATT
Preclinical Neurosciences Section,
Adult Psychiatry Branch,
National Institute of Mental Health,
St. Elizabeths Hospital

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9. Turning was significantly reduced after grafting with substantia nigra [$T(19) = 3.61, P < 0.001$, Scheffé's test]. Turning was not significantly decreased in either the tectal graft group [$T(9) = 1.80, P = 0.075$] or the cortex graft group [$T(10) = 0.38, P = 0.705$]. Apomorphine-induced rotation in the 20 rats with substantia nigra grafts was studied for 6 months after transplantation. There was no further change in rotation rates 7 to 25 weeks after grafting.
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13. Dopamine receptor binding was performed in 8-μm coronal sections of rat brain as previously described (*11*). Serial sections were incubated in $0.17M$ tris-HCl (*p*H 7.4) containing 120 mM NaCl, 5 mM KCl, 2 mM CaCl$_2$, 1 mM MgCl$_2$, and 0.001 percent ascorbic acid for 1 hour at room temperature in the presence of 0.4 nM [^{3}H]spiroperidol and various other drugs. 2-Amino-6,7,dihydroxy-1,2,3,4-tetrahydronaphthalene (ADTN) (1.0 μM) was added to some sections to block binding to dopamine receptors, 0.3 μM cinanserin was added to the incubation medium to block binding to serotonin receptors, and 0.4 μM haloperidol was added to generate blank values. Sections incubated with cinanserin were used in obtaining all the data reported here. After incubation, the sections were washed twice for 5-minute intervals in ice-cold buffer, rapidly dried in a cold airstream, and exposed to ^{3}H-Ultrafilm for 3 months. Quantitative analysis of ligand-binding density in the autoradiograms depended on comparison with a standard curve derived from brain tissue standards containing known amounts of radioactivity (*11*). These standards were coexposed with the experimental sections.
14. J. M. Palacios, D. L. Niehoff, M. J. Kuhar, *Neurosci. Lett.* **25**, 101 (1981); C. Goochee, W. Rasband, L. Sokoloff, *Ann. Neurol.* **7**, 359 (1980); J. R. Unnerstall, D. L. Niehoff, M. J. Kuhar, *J. Neurosci. Methods* **6**, 59 (1982). The tritium-sensitive film was placed on a light board to illuminate individual autoradiograms. The image was digitized by an automatic image analysis system having 512 by 512 pixels and a gray level depth of 256. Next, the dorsomedial quadrant of the striatum on each side of the autoradiogram was selected by using an interactive line-drawing mode to exclude the rest of the image. The program then computed frequency histograms of pixel gray levels in the selected areas and mean gray levels within these areas. All material used for image analysis was coded and evaluated without knowledge of the conditions represented.
15. In vitro binding of various tritiated ligands, such as haloperidol (*6*), apomorphine, and spiroperidol [D. Staunton, B. Wolfe, P. Groves, P. Molinoff, *Brain Res.* **211**, 315 (1981); I. Creese and S. Snyder, *Eur. J. Pharmacol.* **56**, 277 (1979)] has been studied in homogenates of intact and dopamine-denervated striatal homogenates. Depending on the ligand used, increases in maximum binding of 15 to 45 percent have been reported on the lesion side, with little change in dissociation constant values.
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Early Auditory Experience Aligns the Auditory Map of Space in the Optic Tectum of the Barn Owl

Abstract. *Auditory and visual space are mapped in the optic tectum of the barn owl. Normally, these maps of space are in close mutual alignment. Ear plugs inserted unilaterally in young barn owls disrupted the binaural cues that constitute the basis of the auditory map. Yet when recordings were made from the tecta of these birds as adults, the auditory and visual maps were in register. When the ear plugs were removed from these adult birds and binaural balance was restored, the auditory maps were shifted substantially relative to the visual maps and relative to the physical borders of the tecta. These results demonstrate that the neural connectivity that gives rise to the auditory map of space in the optic tectum can be modified by experience in such a way that spatial alignment between sensory modalities is maintained.*

The locations of auditory and visual stimuli in space are represented topographically by multimodal neurons in the optic tectum (superior colliculus). The left-right location (azimuth) of a stimulus is represented along the rostrocaudal axis of the tectum, and the up-down location (elevation) along a mediolateral or dorsoventral axis (*1, 2*). These physiological maps of auditory and visual space are mutually aligned, particularly in the tectum of the barn owl where they correspond, both in azimuth and elevation, to within a few degrees (*1*). This alignment of sensory maps is manifested as a spatial coincidence of the optimal locations of auditory and visual stimuli for exciting single units (*1–3*).

How does the alignment of spatial maps from different sensory modalities come about? The visual and auditory maps are constructed differently. The visual map results from point-to-point projections from the retinas to the tec-

Table 1. Location of centers of auditory best areas relative to centers of visual receptive fields in the rostrodorsal portion of the optic tectum. Misalignments are given as means (and standard deviations). Abbreviations: L, left; R, right; +, up; −, down.

Owl	Ear plugged	Age (days) at which plug was		Misalignment (degrees)		Units (No.)
		Inserted	Removed	Azimuth	Elevation	
Control						
1				0.0 (2.5)	0.0 (3.3)	15
2				0.0 (2.2)	−3.1 (4.8)	20
3				L 1.7 (2.2)	−1.0 (3.5)	11
Experimental						
TO3	Left	41	342			
Plug in place				0.0 (1.5)	−2.3 (7.5)	15
Plug removed				R 10.4 (4.6)	+14.6 (5.9)	8
TO4	Right	40	275			
Plug in place				R 1.8 (2.6)	+4.8 (4.4)	20
Plug removed				L 7.0 (1.8)	−5.8 (9.2)	6
TO6	Right	31	261			
Plug in place				R 4.5 (3.7)	+3.6 (7.7)	22
Plug removed				L 8.8 (1.6)	−10.1 (7.0)	11
TO7	Right	43	202			
Plug removed				L 9.7 (2.5)	−6.1 (9.2)	35

tum, whereas the auditory map is based on systematic variations in the sensitivity of the neurons to differences in the intensity and timing of sound at the two ears (*4*). Thus, the convergence of auditory and visual inputs in the tectum represents an association of specific sets of binaural difference cues with locations in visual space.

To investigate whether the alignment of the auditory and visual maps of space is regulated by sensory experience, I altered the binaural localization cues associated with each location in space, then examined the tecta for induced changes in the auditory map. Young barn owls were studied because these animals recover accurate sound localization behavior after their binaural cues have been disrupted by monaural occlusion (*6*). Owls localize sound in azimuth primarily on the basis of interaural timing cues and in elevation on the basis of interaural intensity cues (*4, 6*); an elevation-dependent, interaural intensity cue is available because the owl's right ear is more sensitive to sounds located up and to the right, and the left ear is more sensitive to sounds located down and to the left (*7*). Chronic monaural occlusion was accomplished by suturing a dense foam-rubber plug (E·A·R, Cabot Corporation) into the external meatus while the owl was anesthetized with halothane and nitrous oxide. The ear plug not only altered interaural timing and intensity, but altered them differently for different frequencies (*8*). Ear occlusion, unlike eye occlusion, does not completely deprive the brain of patterned sensory input, but merely reduces the input and changes its temporal characteristics.

Four barn owls (*Tyto alba*) served as experimental subjects and three as controls. Each experimental bird had one ear plugged (one left and three right) at an age between 31 and 43 days after hatching. The experimental and control birds were raised to maturity (7 months old) in an aviary. As adults, these birds were anesthetized and implanted with a stainless steel chamber in the skull over each optic tectum in preparation for neurophysiological recording. The chambers provided access to the tecta for repeated recording sessions over a period of weeks. Three of the experimental birds were recorded from immediately before and after ear plug removal. The ear plug of the remaining bird (TO7) was removed 4 months before neurophysiological testing was begun.

The recording procedure was the same for all birds. Each owl was anesthetized with ketamine hydrochloride, wrapped in a leather harness, and suspended in a prone position inside a sound isolation chamber containing a speaker movement system (*9*). The owl's head was centered in the apparatus so that its midsagittal and visual planes lined up with 0° azimuth and 0° elevation of the speaker movement system (*10*). Single units were recorded extracellularly (*11*) from the superficial and deep layers of the optic tectum, both of which contain multimodal units in the barn owl (*1*). Wide-band noise bursts (*12*) 20 dB above unit threshold were used to plot auditory receptive fields and best areas. A unit's receptive field was defined as the area within which noise bursts elicited spike activity above background. The best area was the portion of the receptive field where noise bursts elicited more than 50 percent of the maximum spike response. Sizes of receptive fields and locations of best areas were largely independent of sound intensity (*1*). To plot visual receptive fields, a plexiglass hemisphere was brought into the chamber and placed in front of the owl. Bars and spots of positive and negative contrasts were projected onto the hemisphere by a hand-held projector. A unit's visual receptive field was defined as the area in

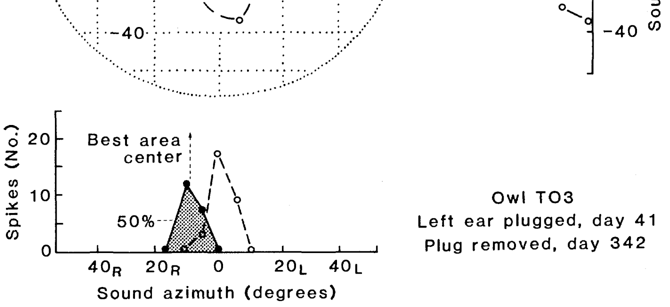

Fig. 1. Auditory receptive field, best area, and visual receptive field of a single unit in the optic tectum of owl TO3 measured before and after a plug in the left ear was removed. The unit was recorded in the deep layers of the right tectum (contralateral to the plugged ear) on the day the ear plug was removed. The grid represents space in double-pole coordinates. The auditory receptive field and best area center measured with the plug still in the ear are plotted with dashed lines and a circled *A*, respectively. The visual receptive field is represented by the hatched rectangle marked with a *V*. The auditory receptive field and best area center of this same unit were measured immediately after the ear plug was removed, and are plotted with solid lines and circled *A* (stippled). The spike counts shown below and to the right are from eight presentations of a noise burst 20 dB above unit threshold. These counts were used to determine the best areas of this unit before and after the removal of the ear plug.

which such visual stimuli elicited an excitatory response. All angular measurements and locations are given in coordinates in which azimuth is measured in degrees right or left from the owl's midsagittal plane, and elevation in degrees above or below the owl's visual plane (*1*). When viewed in line with the origin, isoazimuth and isoelevation lines of this coordinate system appear as perpendicular sets of parallel lines (Fig. 1).

In normal birds, auditory best areas and visual receptive fields are mutually aligned over most of the tectum, but the alignment is most accurate in the rostrodorsal portion, where frontal and upper regions of space are represented (*1*). Table 1 lists the average misalignment of auditory best areas and visual receptive fields for units with visual fields centered at less than 20° in azimuth and between +15° and −5° in elevation. The alignment is nearly perfect, and there is little variation from one unit to the next, as is indicated by the small standard deviations. Because of their consistently close alignment in control birds, the fields of units from the rostrodorsal portion of the tectum were used to evaluate the degree of map misalignment in the experimental birds.

Most units in the tecta of the control owls responded vigorously to auditory and visual stimulation. In contrast, units recorded from experimental birds with ear plugs still in place exhibited elevated auditory thresholds and increased minimum response latencies, and often habituated to repetitive acoustic stimulation. In addition, the degree of bimodality decreased appreciably; most units were driven predominantly or exclusively by one sensory modality.

Despite the general weakening of auditory responses, most units that were responsive to sounds were selective for the location of the source. Of 82 auditory units recorded from birds with ear plugs still in place, only seven units responded to all speaker locations tested, and five responded to all elevations but over limited ranges of azimuth. The remaining 70 units had auditory receptive fields that were limited in both azimuth and elevation.

Of particular significance was that the bimodal units had auditory and visual receptive fields that were fairly well aligned in space. Receptive field data from a single unit recorded in the right tectum of owl TO3 are shown in Fig. 1. With the left ear still plugged, the best area was perfectly aligned in azimuth and 1° above the visual field. The mean misalignments of fields recorded in the rostrodorsal portions of both tecta in each of three experimental birds is shown in Table 1; the mean misalignment for all fields in the three birds was 2.4° ± 2.7° in azimuth and 3.7° ± 6.8° in elevation ($N = 57$). This approximate field alignment in birds experiencing a strong disruption of binaural inputs indicates that these bimodal units had developed specificities for the altered binaural cues that were spatially consistent with their visual receptive fields.

The unit described in Fig. 1 is unique in that its auditory receptive field and best area were measured both before and after the ear plug was removed. On the day this recording was made, the left ear of this owl had been plugged for 301 days. When the ear plug was removed, the auditory field and best area moved abruptly to the right and up, resulting in a gross misalignment between the auditory best area and the visual receptive

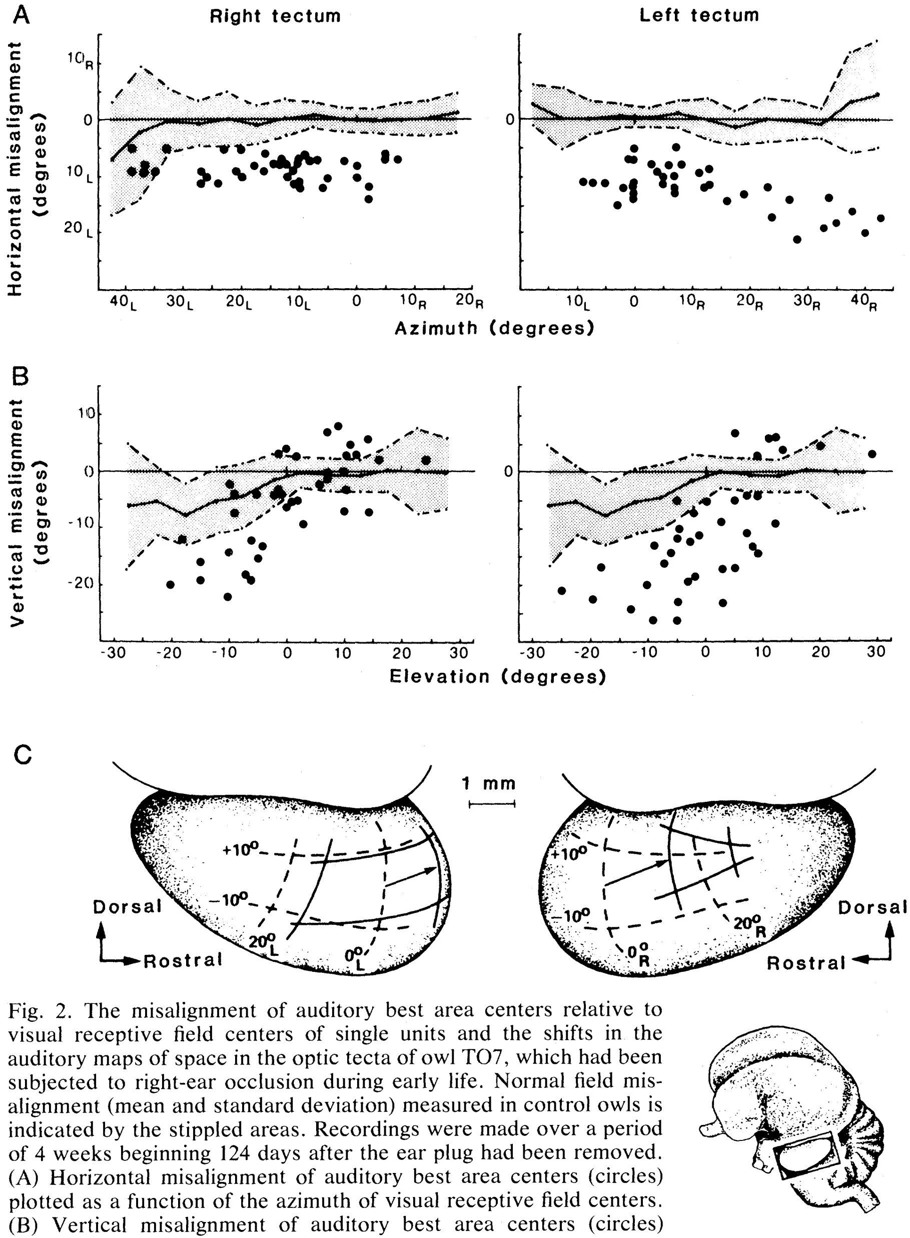

Fig. 2. The misalignment of auditory best area centers relative to visual receptive field centers of single units and the shifts in the auditory maps of space in the optic tecta of owl TO7, which had been subjected to right-ear occlusion during early life. Normal field misalignment (mean and standard deviation) measured in control owls is indicated by the stippled areas. Recordings were made over a period of 4 weeks beginning 124 days after the ear plug had been removed. (A) Horizontal misalignment of auditory best area centers (circles) plotted as a function of the azimuth of visual receptive field centers. (B) Vertical misalignment of auditory best area centers (circles) plotted as a function of the elevation of visual receptive field centers. (C) Shift and distortion of the auditory maps corresponding to the misalignments shown in (A) and (B) depicted on lateral views of the tecta. The dashed coordinate lines represent the auditory map in normal owls (*1*). The solid coordinate lines represent the shifted auditory map in owl TO7. These coordinate lines were derived by calculating the shift in the tectum of the representations of the corner locations; that is, $0°_A$, $+10°_E$; $0°_A$, $-10°_E$; $20°_A$, $+10°_E$; $20°_A$, $-10°_E$, where A and E refer to azimuth and elevation. This was done by computing the mean field misalignments for units with visual receptive fields located within 10° of each location. The mean field misalignment for equivalent locations in control birds was subtracted, yielding the actual induced shift. These shifts were plotted onto the tectal surface through the use of the visual map (*1*). The vectors indicate the shift in the representation of auditory $0°_A$, $0°_E$ in the tecta. The positions and lengths of these vectors were confirmed by electrolytic lesions placed at visual $0°_A$, $0°_E$ and auditory $0°_A$, $0°_E$ on each side. Inset shows the position of the tectum in the owl's brain.

field. The best areas and visual fields of nine more bimodal units (four from the left tectum and five from the right) were measured on this day. Their mean misalignment (auditory best areas relative to visual receptive fields) was right 11.1° ± 4.7° and up 16.6° ± 3.6°; the direction of the elevation shift is expected from the directional asymmetry of the ears (*7*).

Additional recordings were made from the rostral tecta in this owl 3 days and 14 days after removal of the plug. On both days the field misalignments were similar for units in the left and right tecta, so the data were combined. The average misalignment for all units on day 3 was to the right 9.4° ± 3.1° and up 16.1° ± 3.6° ($N = 8$); on day 14 it was to the right 9.4° ± 1.5° and up 12.4° ± 4.4° ($N = 8$). Of these units, eight had visual receptive fields centered at less than 20° in azimuth, and between +15° and −5° in elevation. The average field misalignment for these units is shown in Table 1.

The same procedure was followed with owls TO4 and TO6. In both cases, after the plug was removed auditory best areas were distinctly misaligned with visual receptive fields. However, since in these birds the right ear had been plugged, the auditory fields and best areas moved in the opposite direction—to the left and down relative to the visual receptive fields. Units were recorded until 14 days after plug removal in owl TO4 and until 19 days after plug removal in TO6. In each bird the magnitude of field misalignments decreased slightly in successive recording sessions, but the decrease was within the standard deviations of the samples. Estimates of the misalignment between the auditory and visual maps in these tecta were made by averaging the field misalignments of all units recorded in the rostrodorsal portions of the tecta of each bird (Table 1).

The data indicate that monaural occlusion during early life results in a change in the set of binaural cues to which each unit in the tectum is tuned. These changes enable the bimodal neurons to respond to auditory and visual stimuli in the same spatial location as long as an ear plug is in place. When the plug is removed and binaural balance is restored, the auditory cues to which these neurons respond no longer correspond to the location of their visual receptive fields, but rather to a location away from the side of the plugged ear. The horizontal shift of the auditory fields implies a change in the optimal interaural time delays, and the vertical shift implies a change in the optimal interaural intensity differences necessary to excite these units (*4*).

The shifted auditory maps in the first three experimental birds were stable for as long as 19 days after plug removal. To test the stability of the altered map over a longer period of time, I waited for 124 days after removing the ear plug from owl TO7 before mapping its tecta. Data from this bird were collected over a period of 4 weeks (Fig. 2).

Auditory responses in both tecta were strong with normal thresholds and latencies. The only prominent abnormality was the misalignment of auditory and visual receptive fields: auditory best areas were located to the left of and usually below visual receptive fields. For units in the rostrodorsal portions of both tecta the average misalignment from the visual fields was comparable to the misalignments measured in the two other birds that had been raised with their right ears plugged (Table 1).

Extensive sampling of units throughout the right and left tecta revealed that the field misalignments were not exactly equal on both sides nor in all portions of the same side (Fig. 2). In the right tectum (contralateral to the previously plugged ear), auditory best areas were consistently shifted to the left of visual receptive fields by an average of 8.9°, but their vertical locations ranged from normal in the dorsal tectum to well below normal in the ventral tectum. In the left tectum, horizontal misalignment increased progressively from left 10.2° in the rostral end to left 18.5° in the middle portion of the tectum (visual field centers between right 20° and right 60°). Vertical misalignment was small only in the most dorsomedial portion of the tectum, and it increased dramatically in the middle and ventral portions.

The auditory map was both shifted and distorted by early monaural occlusion (Fig. 2C). The constant horizontal misalignment of fields in the right tectum (Fig. 2A) does not correspond to a linear shift of the auditory map across the tectal surface, because the magnification factor (millimeters of tissue surface per degree of space) in the auditory map decreases sharply toward the caudal end (*1*). For example, the auditory representation of 0° azimuth shifted rostralward by 1.3 mm, while the representation of left 20° azimuth shifted rostralward by only 0.4 mm (*13*). In the left tectum the differential shift of azimuth representations was less severe because the caudally increasing horizontal misalignment of fields partially compensated for the decreasing magnification factor. The greatest distortion in the auditory map was in the representation of elevations. The progressive increase in the vertical misalignments of fields ventrally, that occurred in both tecta (Fig. 2B), represents a dorsally directed compression of auditory elevations, affecting particularly elevations below 0°.

Electrolytic lesions placed in each tectum at the representations of visual 0°_{A}, 0°_{E} and auditory 0°_{A}, 0°_{E} verified the magnitudes of the shifts and established the absolute positions of the coordinate grids in each tectum (vectors in Fig. 2C). Comparing these lesions with equivalent lesions in control birds showed that the auditory map, but not the visual map, had moved in the tecta.

The results demonstrate that the position and relative magnification properties of the auditory map in the optic tectum are regulated by early auditory experience. They do not address the question of whether the experience-dependent modifications take place in the tectum itself or at an earlier stage in the auditory pathway. The persistence of the misaligned auditory maps in adult birds suggests that the mechanism for adjusting neuronal specificities for binaural cues is lost or greatly slowed in the adult nervous system.

ERIC I. KNUDSEN
Department of Neurobiology,
Stanford University School of
Medicine, Stanford, California 94305

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8. Cochlear microphonic recordings from adult, nonexperimental birds were attenuated by 17 to 53 dB from 2 to 10 kHz, and phase-delayed by 0° to 135° from 2 to 10 kHz, depending on sound frequency and the fit of the plug.
9. Details of the speaker movement system, acoustic properties of the chamber and stimuli are given in (*1*). The speaker moved in azimuth along a semicircular track and in elevation as the track pivoted around a horizontal axis.
10. The head was centered through the use of retinal landmarks. The eyes of the barn owl are immobile.
11. Glass micropipettes and tungsten-in-glass electrodes were used.
12. The noise bursts—50 msec in duration with no rise or fall times—were presented once per second. The spectrum of the noise was flat (±2 dB) from 1.8 to 11.0 kHz.
13. The magnification factors come from (*1*). Shift = (8.9°) × (0.15 mm/deg) = 1.3 mm (rostral tectum). Shift = (8.9°) × (0.05 mm/deg) = 0.4 mm (middle tectum).
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