MONAURAL OCCLUSION ALTERS SOUND LOCALIZATION DURING A SENSITIVE PERIOD IN THE BARN OWL¹

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Abstract

Sound localization was disrupted in young barn owls by chronically plugging one ear. Owls that were younger than 8 weeks of age at the time of ear plugging recovered normal localization accuracy while plugged, whereas those that were older than 8 weeks at the time of ear plugging did not. The end of the sensitive period for the adjustment of sound localization accuracy coincides with the maturation of the head and ears, suggesting that the exposure of the auditory system to stable, adult-like acoustic cues could play a role in bringing the sensitive period to a close. The results demonstrate that, early in development, associations between auditory cues and locations in space can be altered by experience.

Animals localize sounds by associating sets of monaural and binaural cues with locations in space. The most reliable cues are binaural, i.e., differences in the timing and intensity of sounds at the two ears. The reliability of these cues results from the fact that they depend only upon the size and shape of the head and ears and do not require assumptions about the properties of the original sound stimulus or the acoustic environment (Searle et al., 1976). Therefore, once the auditory system is calibrated to the passive acoustic properties of the head and ears and correlates frequency-specific binaural differences with locations in space, these binaural cues become unconditional indicators of the location of a sound source.

In the course of normal development, growth of the head and ears increases the range of binaural disparities experienced by the auditory system and alters the correlations of binaural cues with locations in space. Among adults, the size of the head and ears varies; therefore the associations between binaural cues and locations in space differ slightly for each individual. In light of this variability, how does the auditory system establish correct associations between binaural cues and locations in space? One solution might be that calibration of the sound localization circuitry is based upon sensory experience. To explore this possibility we have investigated

the effects of chronically altered binaural cues on sound localization in the barn owl.

Barn owls are an excellent model for studying sound localization: their accuracy is unsurpassed in the animal kingdom; their audible range of frequencies is similar to that of humans; and, unlike most mammals, their external ears are stationary on the head (Payne, 1971; Konishi, 1973; Knudsen and Konishi, 1979; Knudsen et al., 1979). Behavioral experiments have demonstrated that, when barn owls are subjected to chronic monaural occlusion, young birds adjust to the abnormal binaural cues and learn to localize sounds accurately, whereas adult birds do not make this adjustment (Knudsen et al., 1982). These results imply that associations between binaural cues and locations in space can be modified considerably by experience, but only during a restricted sensitive period in early development.

In the present study we demonstrate the extent and nature of this sensitive period by monitoring sound localization accuracy in a large number of owls that had ear plugs implanted at various ages. The sensitive period was found to be relatively discrete, ending less than 2 weeks after the head and ears reach adult size. In the companion paper (Knudsen et al., 1984) we describe the recovery of sound localization accuracy following the removal of ear plugs from owls that had been plugged at an early age. This recovery of accuracy also occurs during a restricted but substantially longer period in development.

We wish to emphasize at the outset that monaural occlusion for the auditory system is not analogous to monocular occlusion for the visual system. Monaural occlusion does not deprive the occluded ear of patterned

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sensory stimulation, it merely attenuates and alters the temporal relationships of frequency components contained in impinging sounds.

Materials and Methods

Nineteen barn owls (*Tyto alba*) served as subjects in the behavioral experiments, and three additional owls were used for recording cochlear microphonics to determine the effects of the ear plugs. Behavioral subjects were removed from their nests between 7 and 12 days post hatching and were raised by hand so that they would remain tame. The growth of the head and ears was followed in eight of these birds by taking periodic measurements of the widths of the skull, facial ruff, and ear canals (Fig. 1).

Ear plugging. Binaural cues were disrupted in the behavioral birds by chronically occluding one ear with a dense foam rubber plug (E.A.R., Cabot Corp.). The effect of such a plug on the sound reaching the tympanic membrane was determined from cochlear microphonic (CM) recordings in three birds. The owls were anesthetized with ketamine hydrochloride, and fine tungsten wires were inserted bilaterally through small holes drilled in the base of the skull. The electrodes were implanted in the scalae vestibuli and on the round windows, and the holes in the skull were sealed with drops of dental cement. The head was secured in a holding device, and the owl was placed in a sound isolation chamber (Industrial Acoustics Co. model 404A). CM responses from the left and right ears were monitored simultaneously on a dual beam oscilloscope while tone bursts were presented from a movable speaker. The linearity of the sound delivery system was calibrated before the experiment. Tone bursts were gated "on" at the zero-crossing of the

sine wave; they lasted 10 msec and were delivered once per second. The sound attenuation caused by an ear plug was measured by the amount of amplification required to bring the CM amplitude up to a criterion level, set in the unplugged state. The criterion amplitude was in the lower portion of the CM's dynamic range. The phase delay (or advance) of sound caused by an ear plug was determined by measuring the induced shift in phase between the CMs from the two ears. The speaker was positioned in front of the owl so that the CMs from the two ears were in phase with both ears unplugged. A high-speed sweep was delayed so that the first cycles of the responses were displayed with maximal time resolution; this enabled us to determine whether the CM was phase delayed or advanced. Then one ear was plugged, and the resulting delay or advance between the CMs was measured by delaying one oscilloscope trace relative to the other until the sine waves again superimposed. The time delay required to superimpose the traces was recorded as the time delay of the CM. In the worst case (2-kHz signals), the measurements were accurate to $\pm 5 \mu\text{sec}$.

Each behavioral bird had one ear plugged at a designated age. The birds were anesthetized with halothane and nitrous oxide while the foam plug was sutured into the external meatus. Plugs were placed in the right ears of 12 owls and in the left ears of 7 owls.

Behavioral paradigm. Behavioral training could begin when the owls reached an age of 50 days; younger birds were incapable of balancing on the perch and eating from the feeder. Training required about 10 days; therefore the earliest age for which data are available is about 60 days.

Sound localization errors were quantified by comparing how an owl oriented its head to sound versus light stimuli. When an owl hears an "interesting" sound, it turns its head with a rapid flick to bring the source of the sound into a frontal region of maximum spatial acuity for the auditory system. This movement also brings the visual axes of the eyes, which are immobile in their sockets, in line with the target. A normal owl orients its head almost identically to either a sound or a light stimulus. A difference between head orientations to sounds and lights among experimental birds was taken as an error in sound localization.

The behavioral tests were conducted with the owl perched in a darkened sound chamber. Sound stimuli were generated by a movable 4-cm speaker; light stimuli were presented with a 3-mm light bulb that was centered in the speaker cone. The speaker and light bulb were attached to a carriage that moved by remote control along a semicircular track. Movements of the carriage along the track altered the azimuth of the stimulus, and rotation of the track around a horizontal axis changed the elevation of the stimulus with respect to the owl.

The behavioral paradigm required the owl to orient its head in response to either a sound or a light stimulus, for which it received a food reward. The reward was not contingent upon the accuracy of the response, only upon its crispness and appropriate latency. To quantify the orientation response of the head, a small mirror was attached to a clip cemented to the skull, and a collimated source of infrared light was directed at the bird. The mirror reflected the infrared beam onto a grid of 0.5°

Figure 1. The external ears of the barn owl are revealed by moving the overlying acoustically transparent facial disc feathers. The sound-collecting surfaces of the external ears are formed by the feathers of the facial ruff. The openings of the ear canals lie behind the preaural flaps. The normal appearance of a barn owl's face (with its facial disc feathers in place) is shown in Figure 2.

increments in a horizontal polar coordinate system. The location of the beam on the grid was monitored using a video camera and stored on video tape for subsequent analysis.

The sound target consisted of repetitive noise bursts of variable amplitude and duration; the light target was a sustained dim glow of the bulb. In both cases the stimulus was presented for up to 2 sec. If the owl did not respond, the stimulus was turned off, followed by a waiting period of about 30 sec. Typically, however, the owl responded immediately with a saccadic head movement and sustained fixation. The stimuli were maintained long enough to allow the owl to maximize its accuracy. The coordinates of the head orientation were then recorded, a reward light was activated, and a food reward was delivered. After every trial the carriage was moved to a new location. In these tests the owl received no feedback regarding the accuracy of its responses.

A single test session consisted of 15 to 25 orientation responses to the sound stimulus and an equal number of responses to the light stimulus. For every response, the location of the stimulus and the coordinates of the final head orientation were recorded. The final orientations of the head were expressed in degrees of azimuth (left-right) and elevation (up-down) relative to the location of the stimulus. Two sets of data points resulted, one for orientations to sounds and another for orientations to lights. A mean and standard deviation were computed for each data set. For normal owls, the distributions of these data sets were virtually identical. However, after we plugged one ear, the owls oriented very differently to sounds and lights. This appeared as a difference between the means of the data sets. The magnitude of this difference we defined as the sound localization error. The scatter of the responses to sounds (standard deviation of the responses to sounds) served as a measure of the precision of sound localization.

Immediately following the plugging or unplugging of one ear, many owls appeared incapable of localizing sounds in one or both dimensions. This was reflected in a large standard deviation in the owl's responses to sound stimuli. However, a large standard deviation did not necessarily indicate that a bird could not localize sounds. An objective assessment of how well the owl was localizing the sound was made by performing a linear regression on the location of the speaker versus the location of the orientation response for both the horizontal and vertical dimensions. For owls that were localizing well, points were tightly clustered around a line with a slope of 1.0. For owls that were localizing poorly, the slope decreased and the fit to the line deteriorated. When a slope was not significantly different from zero (Fischer test; $p < 0.01$), we considered the bird not to be localizing sounds in that dimension. In these cases, no accuracy or precision values were computed.

Results

Growth of the head and ears. Binaural cues depend upon the size of the head and external ears: the larger these structures become, the greater will be the range of differences in the timing and intensity of sound at the two ears. The structure in the owl that is analogous to

the mammalian pinna is the facial ruff (Fig. 1). The ruff, which surrounds the face, is composed of numerous tightly packed rows of extremely dense feathers. Individual feathers are curved, and together they form an acoustically reflective trough-shaped surface that arches from the top of the forehead, behind the opening of the ear canal, then back out along the base of the lower mandible. The ruff on the left side is tilted slightly downward compared to the one on the right. In addition, the preaural flap, which is analogous to the mammalian tragus, is located higher in the ruff on the left side than on the right. These physical asymmetries result in a vertical disparity in the directionality of the two ears at frequencies to which the ruff is an efficient reflector ($f > 3$ kHz): the left ear is more sensitive to sounds from below and to the left, and the right ear is more sensitive to sounds from above and to the right (Payne, 1971). If the ruff is removed, the owl loses its ability to localize sounds in elevation (Knudsen and Konishi, 1979).

As indicators of the growth of the head and ears, we measured (1) the width of the skull at its widest point, (2) the width of the entire facial ruff, and (3) the inner diameter of the external ear canals (Fig. 2). When an owl hatches, its skull is approximately 16 to 18 mm wide, and the future ear canals are mere indentations on the sides of the naked head. In 2 weeks the skull doubles in size and becomes covered down, but the ear canals remain closed and the feathers that will form the facial ruff have not yet appeared. During the third week the ear canals open and the facial ruff begins to grow. The growth of the skull, ruff, and ear canals is extremely rapid and linear for the next 3 weeks. These structures stop growing nearly simultaneously when the owl is 6 to 6.5 weeks of age. Although the body of a 6.5-week-old bird is still covered with down, it has adult-sized head and ears: the skull is 40 to 50 mm wide, the ruff is 82 to 92 mm wide, and the inner diameter of the ear canals is 9 to 10 mm. These data indicate that an owl first experiences stable, adult localization cues when it reaches 42 to 46 days of age.

Acoustical effects of monaural occlusion. The effect of ear plugging on the timing and intensity of the sound reaching the eardrum is shown in Figure 3. Each point represents the median value from at least three determinations of the attenuation or time delay (or advance) of the CM induced by an ear plug. Both ears in each of three birds were measured. The median points of these values, shown by the *dashes* in Figure 3, will be discussed.

The attenuation caused by the plug increased with frequency from 24 dB at 2 kHz to 48.5 dB at 10 kHz. Over the range of frequencies most important for sound localization (4 to 8 kHz; Knudsen and Konishi, 1979), attenuation varied from 26 dB to 39 dB. At frequencies below 5 kHz the attenuation of the CM was considerably less than the sound-attenuating properties of the plug itself. This is to be expected, because the interaural canal in the owl transmits low frequency sounds from one ear to the other (Moiseff and Konishi, 1981a).

The timing of the CM was stable (± 5 μ sec) over changes in sound level through a 60-dB range. The timing of the CM was altered by the ear plug: the CM was delayed at all frequencies except 2 kHz, where there was a 40 μ sec advance. From 4 to 8 kHz the time delay

Figure 2. Growth of the head and ears of the barn owl. The width of the skull and facial ruff and the inner diameter of the external ear canals are plotted as a function of age post-hatching for eight barn owls. These features determine the magnitude of monaural and binaural localization cues. The sketches above are scaled drawings of the owl's face as it appears at 14 and 42 days of age, respectively.

decreased from 52.5 μ sec to 30 μ sec. The large time delays and advances at the lower frequencies are probably the result of the interaction between the sound reaching the eardrum through the interaural canal with that traveling through the plugged ear canal (Coles et al., 1980).

These data indicate that (1) the intensity and temporal properties of sound reaching the eardrum were altered substantially at all frequencies, (2) the effects were frequency specific, and (3) the effectiveness of the plug varied from one plugging to the next. An additional consideration in assessing the behavioral results is that the effectiveness of the plugs may have deteriorated over the period of months that they were worn by the experimental birds.

Localization accuracy and precision in normal owls. The mean error of the auditory responses indicated sound localization *accuracy*, which is the closeness of the responses to the true location of the sound source. The standard deviation of the orientations indicated localization *precision*, which is the repeatability of the response. The accuracy and precision of normal owls lo-

calizing sounds in this system were determined from data collected from six trained owls that were not yet plugged. The localization errors and standard deviations from a total of 22 test sessions (each test session consisting of 19 to 31 sound trials) were averaged. The average localization error was $1.4^\circ \pm 0.8^\circ$ (SEM) in azimuth and $1.2^\circ \pm 0.9^\circ$ in elevation. The average standard deviation (precision) of sound localization was $1.8^\circ \pm 0.6^\circ$ in azimuth and $2.0^\circ \pm 0.7^\circ$ in elevation.

We chose as our criterion of normal accuracy values that were within 2 SD of these averaged control values. Thus, a normal localization error was $\leq 3^\circ$ in azimuth and elevation. Our criterion for normal precision was based on an F-test ($p < 0.01$) of whether the experimental variance was the same as the control variance. For test sessions which included 20 or more sound trials, normal precision corresponded to standard deviations of 3.0° or less in azimuth and 3.7° or less in elevation. Owls were considered to have adjusted their accuracy and precision when their performance was within these criteria levels in two successive test sessions.

Figure 3. The effect of an ear plug on the CM. *A*, The attenuation of the CM caused by an ear plug is plotted against sound frequency. Attenuation was measured by the decibels of sound amplification necessary to return the CM to its pre-plug amplitude. Each point represents the median value of three to six measurements taken from one ear of one owl; both ears of three owls were tested. The horizontal bars represent the medians of these values for each frequency. *B*, The time shift of the CM caused by an ear plug is plotted against sound frequency. The time shift of the CM was measured relative to the CM in the opposite, unplugged ear. The points and horizontal bars represent median values as described for *A*.

Accuracy of localization following monaural occlusion. Owls were plugged monaurally at ages between 27 and 186 days post hatching. Since they could not be tested quantitatively until they were at least 60 days old, the initial effects of ear plugging in very young owls could not be measured. However, it was apparent from the way they oriented to sounds in the laboratory that they had large localization errors (baby owls as young as 14 days of age turned their heads in the general direction of hidden sound sources, indicating at least a crude perception of sound source location).

Only in birds plugged later than 60 days of age was it possible to assess the initial effects of monaural occlusion. These birds were at first unable to localize sounds in either dimension; there was no correlation between the location of the speaker and the owl's orientation response. After a few days or weeks of monaural occlusion, a significant correlation usually appeared first between speaker azimuth and response azimuth, followed later by a correlation between speaker elevation and response elevation. However, birds plugged this late never learned to localize sounds accurately.

The time required for an owl to regain normal sound localization accuracy depended critically on the age at which its ear was plugged (Fig. 4). Owls 1 through 13 (Table I) had one ear plugged before 45 days of age. Six of these had already achieved normal sound localization accuracy by the time they were first measured; five localized with normal accuracy in azimuth but still had a residual error in elevation; and two had residual localization errors in azimuth and elevation. The localization errors in all of these birds were corrected in both dimensions in less than 85 days, and most had corrected in less than 50 days following the insertion of the plug. The most rapid error correction we documented was in owl 4, which was localizing sounds normally in azimuth as soon as it could be trained and tested 27 days after plugging,

Figure 4. The sensitive period for adjusting sound localization accuracy. The number of days required for an owl to regain normal localization accuracy (error less than 3°) is plotted against the age of the owl at the time one ear was plugged. Solid symbols represent the day that normal accuracy in azimuth was attained; open symbols signify the day that normal accuracy in elevation was attained. A downward-pointing arrow indicates that the owl exhibited normal accuracy in that dimension on the first day it was tested. Upward-pointing arrows signify that normal accuracy was never achieved through the last day of testing, indicated above (in fact, these birds made no adjustment of their localization accuracy at all). All birds younger than 60 days of age adjusted their sound localization, whereas no bird 60 days or older adjusted its sound localization.

and finished adjusting its elevation error in the subsequent 5 days (Table I).

Some of the apparent adjustment of sound localization error may have been due to a deterioration of the ear plug, even though the plugs seemed to remain firm.

TABLE I
Summary of auditory histories and experimental results for all owls

Owl No.	Ear Plugged	Age	Time to Recover			
			Accuracy		Precision	
			Azimuth	Elevation	Azimuth	Elevation
		days	days	days	days	days
1	R	28	<46	47	<46	62
2	L	29	46	49	<32	218
3	R	30	<111	<111	>116	>116
4	L	31	<27	32	28	31
5	R	31	<43	46	79	123
6	L	35	<44	<44	<44	<44
7	R	35	<38	<38	<38	<38
8	R	36	<29	41	<29	<29
9	R	39	<60	<60	<60	67
10	L	41	40	61	68	70
11	L	43	<48	<48	55	82
12	R	43	<36	<36	<36	<36
13	R	44	<50	84	<50	<50
14	R	45	69	121	87	102
15	L	54	151	116	<116	<116
16	R	55	96	89	22	62
17	R	60	>111	>111	37	76
18	L	100	>115	>115	29	67
3	R	183	>77	>77	11	>77
19	R	186	>155	>155	79	>155

Because of this possibility, the most reliable indicator of the true extent of physiological adjustment was the localization error induced when the ear plug was removed. In each of the owls that adjusted their sound localization (owls 1 to 16), plug removal resulted in a large localization error toward the side of the ear that had been plugged (Fig. 5A). The errors averaged $8.9^\circ \pm 3.3^\circ$ (SEM) in azimuth and $12.7^\circ \pm 5.9^\circ$ in elevation.

Owls plugged at 45, 54, and 55 days, respectively (owls 14, 15, and 16), took longer to correct their localization errors than did birds plugged before 45 days. Their azimuth and elevation errors persisted for 69, 151, and 96 days and 121, 116, and 89 days, respectively, following insertion of the plug. Because these owls were plugged later in life and their errors lasted longer, we were able to observe the time course of the correction process (Fig. 6A). The rate of error correction was approximately constant, although it slowed appreciably as the error approached the criterion level of 3° . When the ear plugs of these owls were removed some time later, each bird exhibited a large localization error. The average error was $10.7^\circ \pm 4.1^\circ$ (SEM) in azimuth and $11.7^\circ \pm 4.9^\circ$ in elevation.

In contrast to younger owls, owls plugged later than 59 days (owls 17, 18, 19, and owl 3 replug) did not adjust their sound localization accuracy in either dimension in response to monaural occlusion (Fig. 4). Not only did the four owls in this group never achieve normal localization accuracy, they showed no sign of correcting their errors, even after as much as 155 days of monaural occlusion in one case (Figs. 5B and 6B). When these birds had their ear plugs removed, three localized sounds with normal accuracy in both dimensions, and one (owl 3) localized normally in azimuth but had a 4.3° error in elevation. The mean localization errors of these birds following

plug removal was $1.7^\circ \pm 0.9^\circ$ in azimuth in $1.3^\circ \pm 2.0^\circ$ in elevation.

Owl 3 had its right ear plugged twice, once between 30 and 146 days of age and again between 183 and 266 days of age (Fig. 7). This owl was one of the first subjects in this study and was not trained and tested until it was 141 days old, 111 days after its ear was first plugged. Consistent with our data from much younger birds, this owl already had adjusted to its monaural ear plug. When the plug was removed at 146 days of age, the owl exhibited a localization error of 12.4° right and 7.6° up. This error disappeared by 15 days after plug removal. At 183 days of age, the owl's right ear was plugged again and the plug was left in place for 83 days. This time the bird made no apparent adjustment to the plug and it exhibited almost no error when the plug was removed.

Effect of monaural occlusion on precision. An owl's precision often varied substantially from one test session to the next, and trends in the data were difficult to discern. In general, however, monaurally occluded owls localized sounds less precisely than did control owls. The precision of most plugged owls improved slightly with time (Fig. 8), but there was no strict correlation between the age of the owl when plugged and the recovery of normal precision. In four cases, owls eventually learned to localize with precisions that were indistinguishable from those of normal owls; in 13 cases, owls learned to localize with precisions that were still poor, but not significantly different from normal at the $p < 0.01$ level (F-test); and in 3 cases, owls always remained significantly imprecise in at least one dimension throughout the period of testing. The birds in the latter group had been plugged at 30, 183, and 186 days of age, respectively. The owl plugged at 30 days (owl 3, first plugging) learned to localize sounds accurately but never with normal precision. Conversely, owls 17 and 18 achieved normal precision but never corrected their localization errors. In 13 cases where the comparison could be made, normal precision was regained in azimuth sooner than in elevation. Azimuth precision was recovered in a median time of less than 45 days and elevation precision in 68 days.

Discussion

A sensitive period for localization accuracy. Owls that were monaurally occluded before 6 weeks of age adjusted their sound localization relatively quickly (Fig. 4). Those occluded between 6 and 8 weeks of age also adjusted, but the process took longer. All of the birds that adjusted to their ear plugs exhibited large localization errors when their plugs were finally removed (Figs. 5A, 6A, and 7). Owls that were occluded later than 8 weeks of age never corrected their sound localization errors at all, nor did they exhibit errors after their ear plugs were removed (Figs. 5B and 6B). Apparently these older birds were no longer able to alter their associations between auditory cues and locations in space. The data demonstrate that the interpretation of binaural cues by the auditory system remains plastic up to 8 weeks of age.

The sensitive period during which monaural occlusion leads to a change in sound localization ends soon after the head and ears reach adult size. Because these structures determine the correspondence between binaural

Figure 5. Orientation responses to sound sources by one owl plugged early in life and another owl plugged late, showing their responses before (*left*) and immediately after (*right*) removal of the ear plug. Each box contains the data from a single testing session with space represented in degrees of azimuth and elevation relative to the sound target ($\oplus$). Each dot represents an orientation response to the noise stimulus. The left ear of owl 2 was plugged at 29 days of age. The data in *A* show that, 59 days later, owl 2 had adjusted its error and localized sounds accurately (*left*). When its ear plug was finally removed (*right*), this owl exhibited a large localization error to the left and below the target. The data in *B* show the responses of owl 19, which had its right ear plugged at 186 days of age. Data collected 140 days after ear plugging (*left*) indicate that a large localization error still persisted. On the day the ear plug was removed (*right*), owl 19 localized sounds with normal accuracy. Apparently, no adjustment had taken place.

cues and locations in space, it follows that binaural cues change rapidly during their rapid growth over the first 6 weeks of life (Fig. 2). Not until growth stops at 6 to 6.5 weeks of age is the owl's auditory system exposed to stable, adult-like localization cues. At about this same age, adjustment of sound localization in response to monaural occlusion begins to slow, and 2 weeks later monaural occlusion causes no adjustment at all.

Whether it is the age of the bird *per se* or sensory experience that brings the sensitive period to a close cannot be discerned from these experiments; both factors probably play a role. However, certain aspects of the data are consistent with sensory experience being the decisive factor. For example, an owl plugged at 55 days of age adjusted its sound localization over the next 112 days, whereas another owl plugged at 60 days of age did not adjust its localization error at all (Fig. 6). Thus, the ability of the auditory system to adjust for a sound localization error can be preserved beyond 8 weeks of age, if binaural cues in the normal adult range are not being experienced. Apparently, the abnormal sensory conditions caused by monaural occlusion prevent the

termination of the sensitive period, perhaps because sensory feedback indicates an error in sound localization and no longer validates the associations between binaural cues and the locations of sounds in space. Whatever the mechanism, monaural occlusion causes the auditory system to remain in a modifiable state in which binaural cues can be reinterpreted, at least until the sound localization error is eliminated. Assuming that sensory experience does cause the termination of the sensitive period, then the above data imply further that approximately 2 weeks of experience with normal adult localization cues is required to trigger the termination process.

Localization accuracy and precision were usually recovered faster in azimuth than in elevation. Remembering that, for owls, azimuth is derived mainly from interaural time differences and elevation from interaural intensity differences (Knudsen and Konishi, 1979; Moiseff and Konishi, 1981b), this probably reflects the fact that ear plugs affect sound intensity more severely than sound timing (Fig. 3). Over the frequency range of 4 to 8 kHz, which is the most important for sound localization by the barn owl (Knudsen and Konishi, 1979), sounds were

Figure 6. The effect of monaural occlusion on the adjustment of sound localization accuracy for one owl plugged before and another owl plugged after the end of the sensitive period. Sound localization errors are plotted as a function of age for owl 16, plugged at 55 days of age (A), and owl 17, plugged at 60 days of age (B). Owl 16 adjusted its localization error; owl 17 did not. The azimuth (●) and elevation (○) components of the errors are plotted separately. The dashed lines indicate our criterion values for normal accuracy. Representative standard error bars are shown periodically. Stars at the bottom of each graph indicate days on which the owl did not localize the sound in elevation (see "Materials and Methods"). Bars along the bottom represent the auditory history of the owl. The large arrows emphasize the localization error of each owl on the day the ear plug was removed: owl 16 had a substantial error, whereas owl 17 had none.

attenuated by approximately 25 to 40 dB. Such large interaural intensity differences are experienced rarely by an unplugged bird (Knudsen, 1980). On the other hand, over the same range of frequencies, sounds were time shifted by only 30 to 50 μ sec, which is well within the range of 170 μ sec of time delay that barn owls experience normally (Moiseff and Konishi, 1981b). Thus, to recover localization accuracy in elevation, the auditory system had to measure and interpret many intensity difference cues that never would have been encountered under normal conditions, whereas to recover accuracy in azimuth, the auditory system simply had to reinterpret interaural timing differences within an essentially normal range.

Normal sound localization depends on the ability to

discriminate binaural difference cues on the order of decibels and microseconds. Adjustment to occlusion depends not only upon the ability to reinterpret cue/location associations, but also on the ability to resolve small changes in the binaural difference cues. Since sounds reaching the occluded ear were severely attenuated, interaural intensity and time differences had to be evaluated from highly imbalanced signals in the plugged birds. The fact that the owls recovered relatively normal sound localization with one ear plugged indicates that the auditory system has, or can develop, the ability to make fine discriminations of interaural intensity and time differences, even if the signals differ tremendously in magnitude.

The process by which sound localization errors are

Figure 7. Sound localization error of owl 3 plotted as a function of age. Owl 3 had its right ear plugged twice: once at 30 days of age, to which it adjusted, and again at 183 days of age, to which it did not adjust. The azimuth (●) and elevation (○) components of its errors are plotted separately. Stars at the bottom of the graph indicate days on which the owl did not localize sounds in elevation (see "Materials and Methods"). The bar along the bottom represents the auditory history of owl 3.

Figure 8. The effect of monaural occlusion on the precision of sound localization. These data are from owl 17. Localization precision was quantified in terms of the standard deviation of the owl's responses to sound targets. Precision in azimuth (◆) and elevation (◇) are graphed separately. Our criteria for normal precision are indicated by a solid line for azimuth and a dashed line for elevation. The bar along the bottom represents the auditory history of owl 17.

adjusted is a gradual one (Fig. 6A). Thus, it is not the case that incorrect associations are abruptly supplanted by correct ones. Rather, a localization error results in a progressive change in the interpretation of binaural cues along a spatial continuum. This change proceeds until the correct associations are reached.

On the site of neural adjustment in the auditory system. The process of adjusting sound localization must involve a re-evaluation of binaural cues in a frequency-specific manner. The barn owl localizes sounds in elevation on the basis of interaural intensity differences and in azimuth primarily on the basis of interaural ongoing time

differences (Knudsen and Konishi, 1979; Moiseff and Konishi, 1981b). The rate at which these cues change as a function of sound location and the spatial dimensions along which they change most rapidly vary greatly with the frequency of the sound (Knudsen, 1980). Consequently, the spatial information associated with a particular binaural difference value is frequency specific. In addition, the disruption of sound caused by an ear plug is frequency specific: high frequencies are attenuated more and delayed less than low frequencies (Fig. 3). Therefore, the auditory system must adjust its interpretation of interaural intensity and time differences in a fre-

quency-specific manner. Moreover, the horizontal and vertical components of a bird's sound localization error are often corrected at different rates, implying that interaural intensity differences and ongoing time differences are re-evaluated independently. These points suggest that the neural adjustments underlying the adjustment of sound localization must take place at or before a level in the auditory pathway where interaural timing and intensity cues from different frequency ranges are combined.

This observation is important in regard to recent findings that chronic monaural occlusion of young barn owls alters the neural map of auditory space in the optic tectum (Knudsen, 1983, 1984). Monaural occlusion induces a shift of the auditory map which results in a misalignment between the tectal maps of auditory and visual space after the plug is removed. The magnitude of the shift corresponds quantitatively to the sound localization errors reported here for birds subjected to similar conditions. The frequency-specific information that gives rise to the auditory map of space in the tectum first converges at the level of the external nucleus of the inferior colliculus (Knudsen and Knudsen, 1983; Knudsen, 1983, 1984). Therefore, based on the reasoning above, experience-dependent alterations in the auditory pathway must have occurred at or before the level of the inferior colliculus.

Relationship to other studies. The best known and most thoroughly studied sensitive period is the one associated with the development of binocular vision. Animals deprived of binocular vision during early life exhibit profound behavioral deficits as well as changes in the neurophysiology and anatomy of central visual pathways (for a review see Movshon and Van Sluyters, 1981). The experimental manipulation typically used to induce these changes is monocular occlusion. Although similar to monaural plugging as a technique, monocular occlusion is not analogous in its disruption of sensory stimulation to the receptor organ. Monocular occlusion deprives the eye of patterned input, permitting little more than gross changes in ambient luminance to reach the eye. The consequence of monocular occlusion during the sensitive period is an almost complete suppression of afferent activity from the occluded eye (Wiesel and Hubel, 1963, 1965; Hubel and Wiesel, 1970). In contrast, monaural plugging permits ambient sounds to reach the occluded ear, but the sounds are attenuated. A more comparable manipulation in the visual domain is the induction of strabismus (surgically or with prisms) and its effect on stereoscopic vision. To restore stereoscopic vision, spatial correspondences of inputs from the eyes would have to be adjusted based on experience. Although there is evidence that some adjustment does occur early in life, the predominant effect of strabismus is a loss of stereoscopic vision and a dramatic decrease in the binocularity of neurons in the visual cortex (Hubel and Wiesel, 1965; Crewther et al., 1980; Olson, 1980; Van Sluyters and Levitt, 1980). Thus, the visual system seems to respond to discrepant inputs from the two eyes by processing the afferent activity separately.

The auditory system seems to respond differently to disrupted sensory inputs. Instead of suppressing or treating separately the afferent activity from the occluded

ear, inputs from the two ears continue to converge, but the significance of the binaural signals is re-evaluated. Neurophysiological correlates of such alterations have already been demonstrated in the inferior colliculus and optic tectum (Silverman and Clopton, 1977; Moore and Irvine, 1981; Knudsen, 1983). With these as starting points, it may be possible to investigate the neural mechanisms underlying experience-dependent modifications in the auditory system.

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