Capacity for Plasticity in the Adult Owl Auditory System Expanded by Juvenile Experience

Eric I. Knudsen*

In the process of creating a multimodal map of space, auditory-visual neurons in the optic tectum establish associations between particular values of auditory spatial cues and locations in the visual field. In the barn owl, tectal neurons reveal these associations in the match between their tuning for interaural time differences (ITDs) and the locations of their visual receptive fields (VRFs). In young owls ITD-VRF associations can be adjusted by experience over a wide range, but the range of adjustment normally becomes quite restricted in adults. This normal range of adjustment in adults was greatly expanded in owls that had previously learned abnormal ITD-VRF associations as juveniles. Thus, the act of learning abnormal associations early in life leaves an enduring trace in this pathway that enables unusual functional connections to be reestablished, as needed, in adulthood, even when the associations represented by these connections have not been used for an extended period of time.

The central nervous system learns from experience. Early experience gained during "sensitive periods" in development exerts a particularly powerful shaping influence on the brain. For example, experience during a sensitive period can dramatically alter the processing and representation of auditory spatial information in the midbrains of birds and mammals (*1*, *2*). This study demonstrates that, in barn owls, experience during this sensitive period not only shapes auditory space processing in juveniles but also expands the capacity for experience-driven, plastic changes in adulthood.

The auditory map of space in the avian and mammalian optic tectum (also called the superior colliculus) consists of neurons that are tuned for the location of an auditory stimulus (*3*). The auditory spatial tuning of these neurons results from their tuning for spatial cues, such as ITDs and interaural level differences, that vary systematically with the location of a sound stimulus relative to the head and ears (*4*). Neurons in the optic tectum that respond to both auditory and visual stimuli have mutually aligned auditory and visual spatial tuning (*3*). This alignment of auditory with visual spatial tuning represents the association of particular values of auditory spatial cues with the locations in the visual field that produce them.

In both birds and mammals, the auditory-visual associations that are represented by the spatial tuning of tectal neurons are shaped extensively by early experience (*1*, *2*). During a sensitive period, the normal tuning of tectal neurons for auditory spatial cues can be adjusted to compensate for idiosyncrasies in the auditory-visual relationships experienced by the individual. These adjustments maintain accurate alignment of the auditory and visual maps of space in the tectum. For example, in juvenile barn owls, the value of ITD to which a tectal neuron is tuned can be shifted by exposing the animal to a chronic horizontal displacement of the visual field with prismatic spectacles (*1*). Over 6 to 8 weeks, tectal neurons become tuned to the values of ITD that correspond with their optically displaced VRFs, an adjustment that is adaptive because it realigns the auditory map with the optically displaced visual space map (*5*). In contrast, in adult owls (older than about 200 days) that have grown up experiencing only normal correspondences between ITD values and VRF locations, equivalent experience results in little or no adaptive adjustment of ITD tuning (*6*).

In this study, the capacity for ITD tuning adjustment was compared in two groups of adult owls (owls older than 1 year). Owls in one group ($n = 2$) experienced only normal ITD-VRF correspondences throughout the sensitive period (*7*). Owls in the second group ($n = 3$) learned abnormal ITD-VRF associations while they were juveniles as a result of wearing displacing prisms that shifted the visual field 23° to the right (R23°) (*8*). After these abnormal associations had been learned, prisms were removed and ITD tuning returned to normal. Thus, both groups of adult owls began these experiments with normal ITD-VRF associations expressed in the tectum.

The capacity of tectal neurons to alter ITD tuning was assessed in both groups of owls by exposing them to a chronic R23° displacement of the visual field (*9*). The results of this experiment for a representative owl from each group are shown (Fig. 1). In both owls, ITD tuning was normal before prisms were mounted (Fig. 1A). The ITD tuning curves (Fig. 1A, left) were recorded

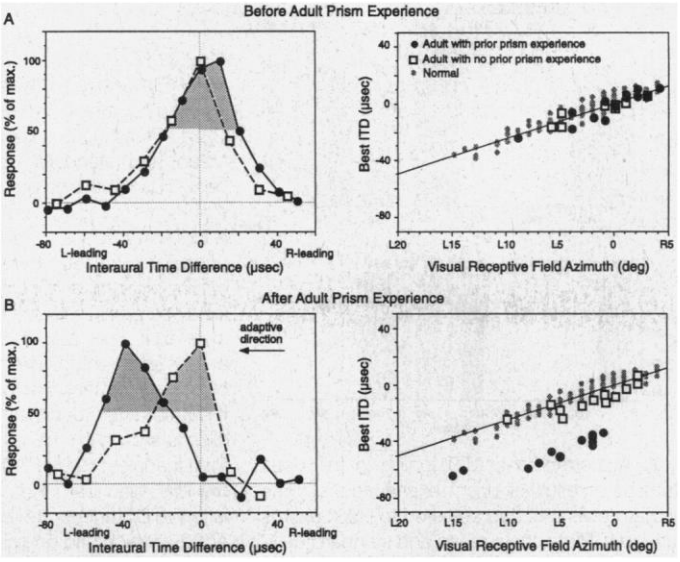

Fig. 1. Effect of experience with R23° prisms on ITD tuning in the optic tecta of two adult barn owls. One adult (Pr5) had experienced R23° prisms as a juvenile (filled circles); the other adult (Ad222) had not (open squares). (**A**) ITD tuning before adult prism experience. (Left) Representative ITD tuning curves for matched sites in the optic tectum of the two owls. The VRFs were located at 0° azimuth for Pr5 and at L1° for Ad222. Shaded area represents responses greater than 50% of the maximum response; the centers of these ranges of ITDs are the best ITDs for these sites. Best ITDs were 0 and L2.5 µs for the Pr5 and Ad222 sites, respectively. (Right) Best ITD versus VRF azimuth for populations of sites from owl Pr5 (filled circles), Ad222 (open squares), and five normal barn owls (shaded dots). Diagonal line represents the regression of best ITD on VRF azimuth for data from the normal owls. The equation for the line is $y = 2.5x$. Deviations from this line were interpreted as shifts from normal ITD tuning. (**B**) Data comparable to those shown in (A), collected after the two owls experienced R23° prisms. Data from Pr5 were collected after 17 days of prism experience, beginning when the owl was 785 days old. Data from Ad222 were collected after 183 days of experience, beginning when the owl was over 2 years old. Tuning curves on the left are from matched sites with VRFs located at L1° and R1° azimuth for Pr5 and Ad222, respectively.

Department of Neurobiology, Stanford University School of Medicine, 299 Campus Drive, Fairchild Building D259, Stanford, CA 94305–5125 USA.

*To whom correspondence should be addressed. E-mail: eknudsen@leland.stanford.edu

from equivalent locations in the tectum with VRFs centered on 0° azimuth (*10*). The best ITD (*11*) for both sites was about 0 μs, which is the normal value predicted for these sites based on the correlation of best ITD with VRF location measured in normal owls (Fig. 1A, right, shaded dots and regression line). The relationship between best ITD and VRF location measured in these two birds before they experienced prisms as adults (*12*) is summarized (Fig. 1A, right); the data follow the normal relationship.

ITD tuning in the tecta of these animals after they were exposed to R23° prisms is shown (Fig. 1B). Both birds were more than 2 years old when the prisms were mounted. The owl with no prior prism experience (open squares) wore the prisms for over 6 months, after which best ITDs had shifted toward left-ear leading values (the adaptive direction for R23° prisms) by an average of only 4 μs. In contrast, the owl with prior prism experience (filled circles) wore prisms for only 17 days, after which best ITDs had shifted in the adaptive direction by an average of 33 μs.

The ITD tuning adjustments that occurred in the tecta of the three owls that had experienced R23° prisms previously as juveniles are documented (Fig. 2). As adults, owl Pr4 experienced only R23° prisms, whereas owls Pr5 and Pr6 also experienced L23° and R34° prisms. In all three owls, the capacity to adjust ITD tuning in response to R23° prisms as adults was increased by experience with R23° prisms as juveniles, as indicated for owl Pr5 (Fig. 1).

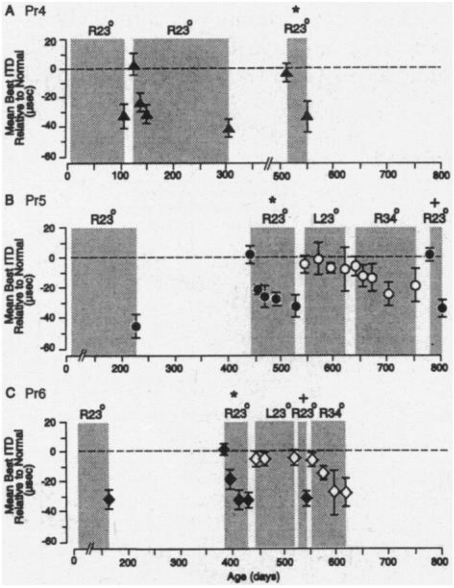

Fig. 2. Adjustments of ITD tuning in the optic tectum as a result of prism experience in three adult barn owls that had adjusted to R23° prisms as juveniles. Plots show mean and standard deviation of the shift in best ITDs relative to predicted normal, derived as shown in Fig. 1B, measured at various ages. Shaded regions indicate periods of prism experience. Filled symbols indicate data collected during exposure to R23° prisms; open symbols represent data collected during exposure to prisms of some other strength or direction. Asterisks and crosses indicate the first and second exposures, respectively, to R23° prisms that are replotted in Figs. 3 and 4. Negative ITD values indicate left-ear leading ITDs.

The expanded range of ITD tuning plasticity in adult owls that had previously adjusted ITD tuning as juveniles is shown in greater detail (Fig. 3). In the two adult owls that had experienced only normal ITD-VRF correspondences throughout the sensitive period, more than 6 months of experience with 23° prisms led to a mean shift in ITD tuning of only 4 μs in each owl (Fig. 3A, open symbols). Population tuning curves, which are the average of all ITD tuning curves for the sample (*13*), indicated that this small shift in best ITDs was due to a consistent increase in neuronal responses to more left-ear leading values of ITD (Fig. 3B).

In contrast, in the three adult owls that previously had adjusted to R23° prisms as juveniles, ITD tuning shifted rapidly and over a much larger range. Reexposure to R23° prisms in adulthood (Fig. 2, asterisks) led to average shifts in ITD tuning of about 30 μs within 30 days (Fig. 3A; data replotted from Fig. 2). Population tuning curves revealed that these shifts were due to both the acquisition of strong neuronal responses to adaptive values of ITD that were previously ineffective in driving neurons and the elimination of responses to normal values of ITD that were previously strongly excitatory (Fig. 3C). The magnitude of the shifts in ITD tuning that occurred in adulthood after 60 days of prism experience was equivalent to the magnitude of shifts that had occurred previously when they were juveniles in two of the three owls (Fig. 3A, filled diamonds and triangles). In the third owl (Fig. 3A, filled circles), the shift after 60 days of experience was abnormally large, and after 90 days it was even larger (Fig. 2B). Nevertheless, these shifts were smaller than the shift that was observed after 213 days of experience as a juvenile.

The extent of the expanded range of possible ITD-VRF associations was tested in two owls (Fig. 4). First, I addressed the question of whether early experience with R23° prisms had expanded the range of adult plasticity to include shifts of ITD tuning in both directions—that is, whether unusual associations with more right-ear leading as well as with more left-ear leading ITDs could be established. The R23° prisms were removed from both owls and ITD tuning returned to normal (Fig. 2, B and C). Then, L23° prisms were mounted. Over the periods of more than 75 days that the owls wore these prisms (Fig. 4, open symbols), ITD tuning in the tectum showed virtually no sign of adjusting toward right-ear leading ITDs, the adaptive direction for L23° prisms. Thus, the expand-

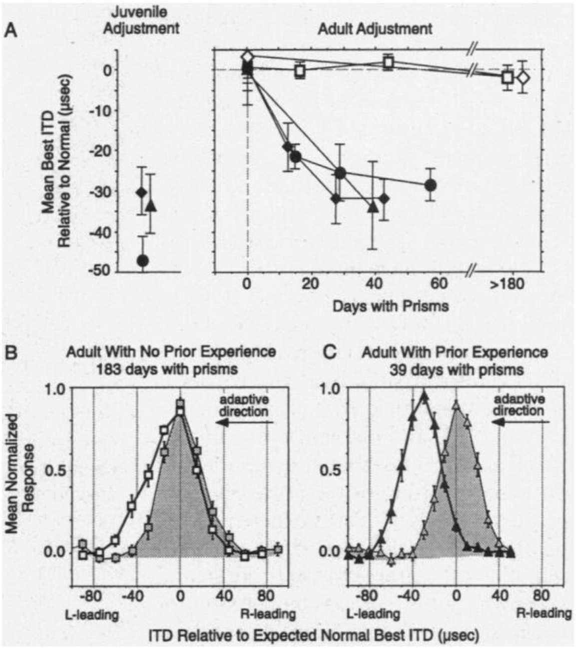

Fig. 3. Effect of early experience with R23° prisms on the capacity to adjust ITD tuning in response to R23° prisms in adult barn owls. (**A**) Mean and standard deviation of best ITDs relative to predicted normal values from Fig. 2 are plotted as a function of days of prism experience for two adult owls that had had no prior experience with prisms (open symbols) and for three adult owls that had adjusted to R23° prisms as juveniles. The magnitude of the adjustment that occurred in the latter owls when they were juveniles is shown on the left. Owl Pr4, filled triangles; owl Pr5, filled circles; owl Pr6, filled diamonds. (**B**) Population ITD tuning curves for owl Ad222, which had no prism experience as a juvenile, measured before (shaded squares) and after (open squares) 183 days of experience with R23° prisms as an adult. Direction of adaptive shift is indicated by the arrow. Bars indicate standard error of the mean. Comparable population tuning curves for the other adult owl with no prior prism experience looked the same. (**C**) Population ITD tuning curves for owl Pr4, which had adjusted to R23° prisms previously as a juvenile, measured before (shaded triangles) and after (filled triangles) 39 days of experience with R23° prisms, beginning at 511 days of age. Data are plotted as described in (B). The comparable population tuning curves for owls Pr5 and Pr6 were essentially the same.

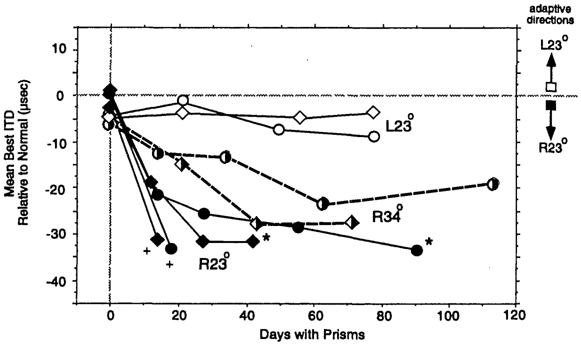

Fig. 4. Range and rate of ITD tuning adjustments in the optic tecta of two adult owls that had adjusted to R23° prisms as juveniles. Mean best ITD relative to the predicted normal value, from Fig. 2, is plotted as a function of days of experience with prisms for owl Pr5 (circles) and owl Pr6 (diamonds). Open symbols show the effect of prisms that displaced the visual field in the opposite direction (L23°) from the prisms they experienced as juveniles. Half-filled symbols show the effect of R34° prisms that displaced the visual field 50% further than the R23° prisms they had experienced previously. Solid symbols show the effect of R23° prisms in adulthood; asterisks and crosses indicate results from the first and second adult experiences, respectively, with R23° prisms. The ages during these manipulations are shown in Fig. 2. Negative values indicate left-ear leading ITDs.

ed range of adult plasticity was limited to the direction of ITD tuning adjustment that was learned during the sensitive period.

A final experiment tested whether early experience with R23° prisms had enabled unlimited adjustment toward left-ear leading ITDs, as opposed to shifts limited to the same magnitude as that achieved during juvenile exposure to prisms. In an attempt to shift ITD tuning beyond the range that was learned as a result of juvenile experience, the owls were fitted with R34° prisms (Fig. 4, half-filled symbols). In both owls, ITD tuning adjustment in response to R34° prisms progressed more slowly and the final magnitude of adjustment was, if anything, less than the magnitude of adjustment that resulted from experience with R23° prisms, tested both before (Fig. 4, asterisks) and after (Fig. 4, crosses) this experience. These data suggest that the range of potential ITD-VRF associations in the adult animals was limited to the associations that had been established by experience during the sensitive period.

The data demonstrate that experience during a sensitive period establishes functional connections that leave an enduring trace in the adult central nervous system. This trace may be anatomical in nature. Prism experience has been shown to induce changes in the pattern of axonal projections in the ITD pathway leading to the optic tectum, changes that can account for the shift in ITD tuning observed in the tectum (*14*). This unusual anatomical projection coexists with the normal anatomical projection in birds with shifted ITD maps. If this projection were to persist in the adult after ITD tuning returned to normal, then the adult capacity to relearn the abnormal ITD-VRF associations could result from the reactivation of this previously established, anatomical circuitry. An attractive feature of this model is that it accounts for the sensitive period in this pathway simply as the period when experience can cause the formation of anatomical projections.

Regardless of the underlying mechanism, the results show that, in the midbrain auditory space-processing pathway, experience in adulthood can reestablish functional connections that were established previously by experience during the juvenile period, even though these functional connections may not have been used for a long time. The persistence of the effects of experience despite disuse is a characteristic of many sensitive periods, including song learning in birds (*15*), sexual imprinting in birds and mammals (*16*), and language learning in humans (*17*). The space-processing pathway in the barn owl offers the opportunity to study the cellular and molecular basis for such persistent effects and the signals that instruct them. Because in this pathway the capacity to reestablish previously learned functional connections is persistent, learning during the sensitive period together with innately determined patterns of connectivity determine the repertoire of functional states that the central nervous system can assume in response to adult experience.

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7. The richness of the environment provided by housing conditions has a profound influence on the capacity for plasticity. In this study, the owls lived in group flight rooms, which provide the most conducive conditions for plasticity of those previously tested. The sensitive period for the effects of prism experience on the auditory spatial tuning of tectal units was established with owls housed in these aviaries (*6*).
8. Prism-rearing began at 15 days of age for each owl, just as the eyelids first opened. Fresnel prisms were mounted in wire frames that were sutured to the scalp while the animal was anesthetized with halothane and nitrous oxide. The baby owls were housed together in a nest box. When the owls were about to fledge, at 60 days of age, the prisms were mounted in metal frames that were bolted to the animal's skull with a threaded nut that was cemented to the skull while the animal was anesthetized. At this time, the owls were released into a large group aviary.
9. Preparation of the animals, acoustic stimulation, and electrophysiological techniques were the same as reported previously (*1*, *5*).
10. VRF locations were measured with prisms removed by presenting dark or light bars projected onto a calibrated tangent screen located 1.9 m in front of the owl.
11. Unit tuning for ITD was measured by delivering computer-generated noise bursts (4 kHz high-pass filtered; 50 ms duration; 0 ms rise/fall time; 1 per s; 20 to 30 dB above threshold; optimized ILD) via matched earphones. Each value of ITD was presented 10 to 20 times in a randomized, interleaved order. ITD tuning at each site was represented by the "best ITD," the center of the range of ITD values that evoked greater than 50% of the maximal response for that site. A "predicted normal best ITD" was derived from the location of the site's VRF, using a regression of best ITD on VRF location that was based on a large population of normal data (Fig. 1B). ITD tuning adjustment was quantified as the difference between measured best ITD and the predicted normal best ITD, averaged across all sites.
12. ITD-VRF associations were assessed periodically by measuring ITD tuning and VRF locations at 9 to 19 recording sites sampled systematically across the optic tectum. Sites were sampled at a minimum interval of 400 μm in the rostroventral tectum. This portion of the tectum, which represents visual field locations within ±15° of the midsagittal plane and from 0° to −20° in elevation, contains neurons that shift their auditory tuning most reliably in young owls.
13. Population ITD tuning curves were derived from the sample of ITD tuning curves measured in a single experiment. To combine tuning curves across sites, the ITD tuning curve for each site was normalized to the maximum response. Then, the values of ITD that were tested were transformed into values of ITD relative to the predicted normal best ITD for that site, based on the site's VRF. The normalized responses for standard values of ITD (either 10- or 15-μs intervals) relative to predicted normal best ITD were interpolated. These interpolated responses were then averaged across all sites for each standard value of ITD.
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