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Visual Instruction of the Neural Map of Auditory Space in the Developing Optic Tectum

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Neural maps of visual and auditory space are aligned in the adult optic tectum. In barn owls, this alignment of sensory maps was found to be controlled during ontogeny by visual instruction of the auditory spatial tuning of neurons. Large adaptive changes in auditory spatial tuning were induced by raising owls with displacing prisms mounted in spectacle frames in front of the eyes; neurons became tuned to sound source locations corresponding to their optically displaced, rather than their normal, visual receptive field locations. The results demonstrate that visual experience during development calibrates the tectal auditory space map in a site-specific manner, dictating its topography and alignment with the visual space map.

THE BRAIN CREATES A MAP OF AUDItory space by systematically organizing neurons according to their tuning for sound localization cues [such as interaural differences in timing and intensity (1)]. In contrast, the brain's map of visual space derives from a point-to-point projection from the retinae. Yet in the optic tectum (superior colliculus), auditory and visual maps of space share the same topography and are mutually aligned (2, 3) so that auditory or visual stimuli originating from a given object in space activate neurons at a single tectal site. This alignment is likely to be critical to the role of the optic tectum in redirecting the eyes toward sources of sensory stimuli (4).

The matching of auditory and visual space maps results in part from the remarkable plasticity of the auditory spatial tuning of tectal neurons, particularly in developing animals but also in adults (5–9). In adult monkeys, the auditory spatial tuning of some tectal neurons is altered during voluntary eye movements, thereby tending to maintain the alignment of the auditory and visual space maps even when the eyes are turned in the head (7). In young ferrets, surgically induced deviation of the eye results in a similar adaptive change in the auditory spatial tuning of tectal neurons (8). However, in the latter case it is not clear whether the change in spatial tuning is due to the effects of abnormal eye position or is
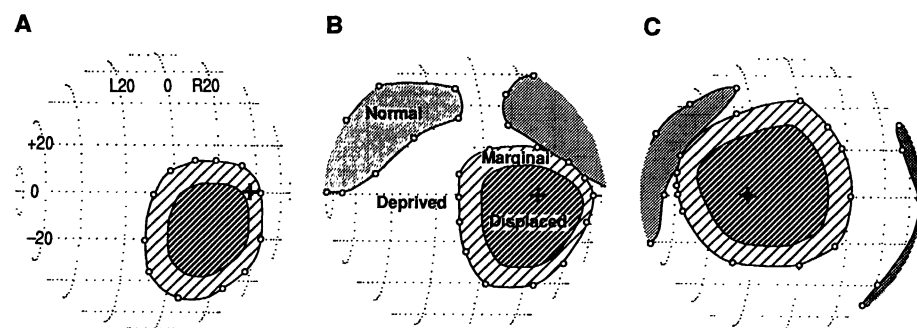
a result of the chronic displacement of the visual field. In this study, we dissociated the effects of eye position from those of displaced vision by raising owls with prismatic spectacles. The results demonstrate a powerful instructive influence of vision on the developing auditory space map.

Lightweight spectacle frames containing matched Fresnel prisms were attached to three barn owls at 12 to 15 days of age, just as the eyes were beginning to open for the first time. Because barn owls cannot move

their eyes more than 2° to 3° (10), prismatic spectacles exposed distinct portions of the retinae to relatively constant conditions of displaced vision, blocked vision, or normal vision (Fig. 1). The prisms displaced the central portion of the visual field 34° to the left (L34°) in owl 1, 23° to the left (L23°) in owl 2, and 23° to the right (R23°) in owl 3. The owls were raised together with other siblings in an environment rich in visual and auditory stimuli.

We assayed the effects of rearing with prisms on the auditory space map by comparing the locations of auditory and visual receptive fields of extracellularly recorded units. Auditory receptive fields were represented by the center of the best area, the area of space from which the sound stimulus elicited greater than 50% of the maximum number of action potential responses (Fig. 2). In normal owls, auditory best areas and visual receptive fields align well, on average within 2° in azimuth and 5° in elevation (2, 9). Because visual receptive field locations in the tectum do not seem to be altered by prism rearing or visual deprivation (9, 11), the alignment of auditory best areas with visual receptive fields provided a means to assess abnormal auditory spatial tuning in the prism-reared owls.

The auditory and visual receptive fields of a single unit from the owl raised with L23° prisms are shown in Fig. 2. The auditory-visual misalignment (bold arrow) approximately matched the displacement of the unit's visual receptive field caused by the prisms. A prismatic displacement of an owl's

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Fig. 1. Visual conditions in different regions of space for the prism-reared owls 1, 2, and 3 (A, B, and C). We determined the borders of each region by sighting the retinae with an ophthalmoscope from calibrated locations relative to the head with the head fixed in standard position (2); the precision of the measurements is 2°. The normal zones (stippled) indicate areas of space from which at least one retina could be sighted without the line of sight passing through the prisms. The deprived zone (no shading), which constitutes a large portion of the frontal hemifield, indicates areas of space from which neither retina could be seen, the line of sight being obstructed by feathers, the spectacle frames, or the optical properties of the prisms. The displaced zone (heavy diagonal lines) indicates the area of space from which at least one retina could be sighted through the prisms. A marginal zone (sparse diagonal lines), corresponding to a 10°-wide boundary between the displaced and deprived zones, represents approximately the portion of the visual field that was subjected to variable visual conditions, because of factors such as small eye movements and changes in the distance of the prisms from the eyes during growth. In all figures, locations are represented from the owl's perspective as angles relative to the midsagittal plane (azimuth) and the visual plane (elevation) measured from the center of the head. The projections of the optically displaced visual axes are indicated by the solid crosses. The normal zones for owl 1 were similar to those for owls 2 and 3, but were not measured.

Fig. 2. Shifted auditory spatial tuning of a tectal unit caused by prism rearing. Plotted on a globe of space are the auditory receptive field (vertical elliptical area) and visual receptive field (vis RF, indicated by boxes labeled for prisms on and prisms off) of a superficial layer unit recorded in owl 2 (prisms: L23°). The responses of the unit to broadband noise bursts presented from various locations are shown at the bottom and to the right. The best area is indicated by the stippled portions of these location-response profiles. The center of the best area is marked by arrows in the profiles and by a circled A on the globe. Visual receptive fields were measured with the prisms off and with the prisms on in response to bars and spots of light projected onto a calibrated, translucent hemisphere (radius, 57 cm). A vector indicates the discrepancy between the center of the auditory best

area and the center of the visual receptive field without prisms (auditory-visual misalignment); in normal owls, auditory-visual misalignments are consistently small (2) (Fig. 3D). The owls were prepared for repeated recording experiments as described (2, 9). Before an experiment, the owl was anesthetized with ketamine HCl (20 mg per kilogram of body weight) and tranquilized with diazepam (5 mg/kg). Because there were no incisions or pressure points, ketamine injections were not repeated unless the animal exhibited discomfort. The owl was placed in a sound-attenuating chamber containing a loudspeaker that moved by remote control in a perimetric system (2). Auditory spatial tuning was measured with the prisms in place with 50-ms broadband noise bursts presented at 20 dB above the unit's threshold. Responses to ten repetitions of the noise burst were collected at 5° or 10° intervals in azimuth and elevation across the auditory receptive field. Auditory best areas and visual receptive fields did not significantly differ in size from those observed in normal owls (2, 9): the mean size of auditory best areas was 21° ± 10° (SD) in azimuth and 36° ± 20° in elevation (five sites out of 234 were not tuned for elevation); the mean size of visual receptive fields was 7° ± 6° in azimuth and 8° ± 8° in elevation (n = 186).
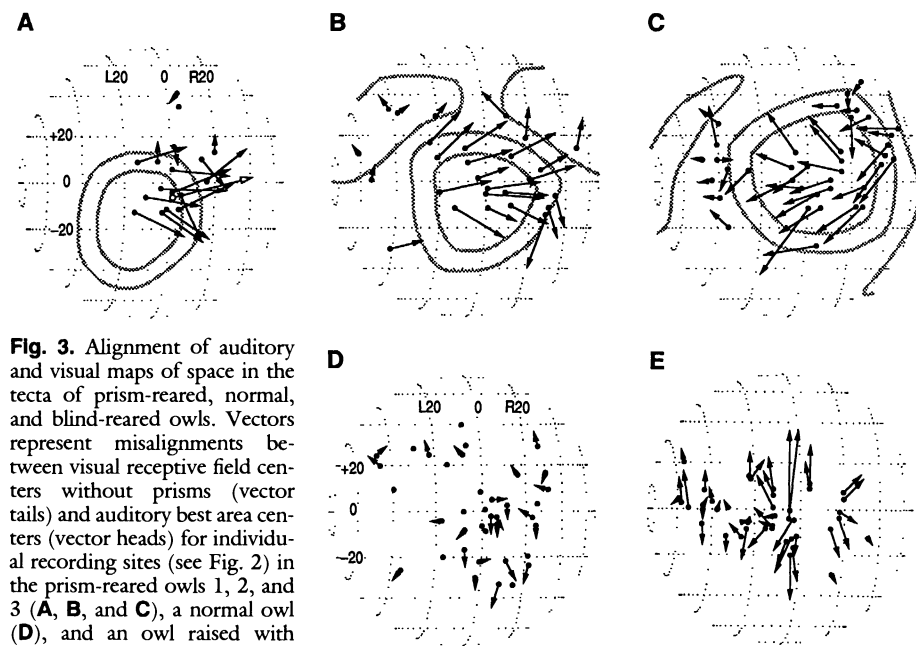
Fig. 3. Alignment of auditory and visual maps of space in the tecta of prism-reared, normal, and blind-reared owls. Vectors represent misalignments between visual receptive field centers without prisms (vector tails) and auditory best area centers (vector heads) for individual recording sites (see Fig. 2) in the prism-reared owls 1, 2, and 3 (**A**, **B**, and **C**), a normal owl (**D**), and an owl raised with both eyelids sutured closed (**E**). The data from the normal and blind-reared owls are provided for comparison and have been published (9). Included on the plots for the prism-reared owls (A through C) are the boundaries of the displaced, marginal, deprived, and normal visual zones (defined in Fig. 1) plotted in retinotopic coordinates, that is, with the displaced and marginal zones shifted by the amount of the prisms. Plotting the zones in this fashion indicates the locations of visual receptive fields that were shifted by the prisms. The data from the prism-reared owls are representative of measurements made after about 85 days of age. The total number of bimodal recording sites in each bird was 28, 99, and 59 in owls 1, 2, and 3, respectively. Overlapping vectors are not shown. The highlighted (open symbol) vector in (A) is based on data from a recording site at the rostral end of the right tectum, where the azimuths of auditory best areas were centered up to 40° into the ipsilateral hemifield. All other vectors in this plot represent recording sites from the left tectum, where auditory best areas were essentially limited to the contralateral hemifield.

visual field in one direction (in this case to the left) corresponds to a displacement of unit visual receptive fields in the opposite direction (in this case to the right).

Representative samples of the auditory-visual misalignments in owls 1, 2, and 3 after at least 70 days of prism experience are
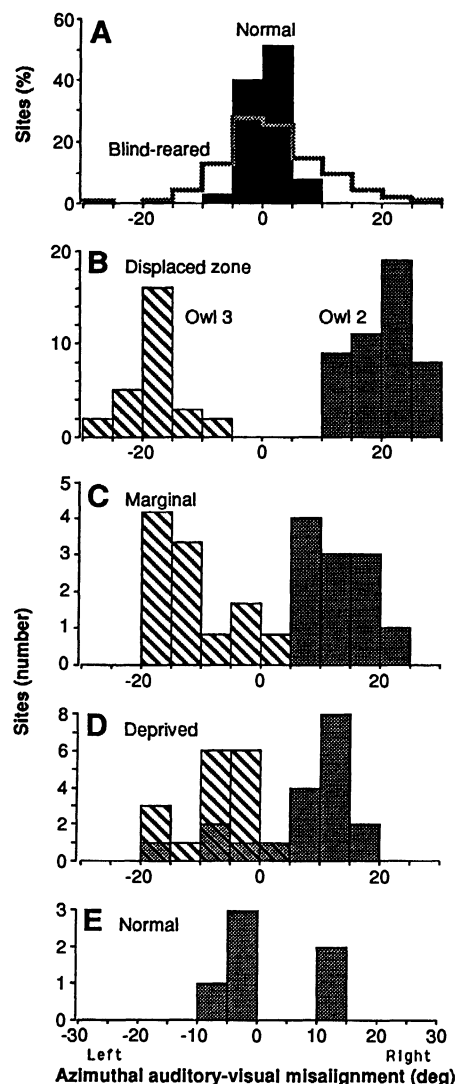
Fig. 4. Frequency distributions for the azimuthal component of auditory-visual misalignments (auditory azimuth minus visual azimuth) grouped according to visual conditions. (**A**) Data from 102 bimodal recording sites in three normal owls (solid bars) and from 332 sites in six blind-reared owls (stippled lines), normalized for total number of sites [data from (9)]. (**B** through **E**) Data from all bimodal sites in owls 2 (stippled) and 3 (cross-hatched), separated according to the visual conditions to which the units were subjected (see Fig. 3). The auditory-visual misalignments of units with visual receptive fields in the prismatically displaced zones were significantly larger (ANOVA; P < 0.05) than those of units with visual receptive fields located in the deprived zones, and the misalignments for both of these populations were significantly larger than those in normal and blind-reared owls; the misalignments of units in the normal zone were not statistically different from those observed in normal or blind-reared owls.

summarized in Fig. 3. Misalignments varied greatly yet systematically across the tecta in each bird. In the visual representation of peripheral locations (caudal tectum), where vision was either normal or obstructed (Fig. 1), auditory-visual misalignments were relatively small. In contrast, in the visual representation of frontal space (rostral tectum), which was subjected to a displaced visual field (Fig. 1), auditory-visual misalignments were abnormally large, ranging up to 38° in azimuth, and were always in the same direction as the optical displacement of the visual receptive field (to the right in owls 1 and 2 and the left in owl 3) (Fig. 3, A through C). A correlate of this systematic shift in auditory spatial tuning was that the extent of the auditory map at the rostral end of the tectum was dramatically different on the two sides of the brain. In the normal map, which is primarily of contralateral space, auditory best area centers of neurons in the rostral tectum represent locations up to 17° into the ipsilateral hemifield (2). By contrast, in owl 1 neurons in the rostral tectum on the right side represented locations up to at least 40° into the ipsilateral hemifield, whereas neurons in the rostral tectum on the left side represented locations up to only ~0° (Fig. 3A). These results demonstrate that during development the range of auditory locations that come to be represented in each tectum is selected by visual instruction from a wider range of possible locations.

The auditory maps in the prism-reared birds were not only shifted in azimuth, but were "stretched" in elevation as well: units with visual receptive fields located above the visual plane tended to have auditory best areas located higher than visual receptive fields (upward vectors, Fig. 3, A through C), whereas units with visual receptive fields located below the horizon tended to have auditory best areas that were abnormally low (downward vectors). This type of distortion in the representation of auditory elevation is observed frequently in owls

raised without vision (Fig. 3E) (9). The deprivation-like pattern of misalignments observed in the prism-reared birds probably reflects the fact that the prisms not only displaced the visual image but degraded it slightly as well.

The large azimuthal misalignments that were observed in the rostral tectum of the prism-reared owls do not occur in normal or visually deprived owls (2, 9) (Fig. 3, D and E). We conclude, therefore, that at least this component of the auditory-visual misalignments was caused specifically by the prismatic displacement of the visual field. The vector plots (Fig. 3, A through C) suggest that the magnitude of this effect depended on the visual conditions that existed in the region of space containing a unit's visual receptive field. To explore this suggestion quantitatively, we grouped all of the data from owls 2 and 3 (the most extensively studied) according to whether the visual receptive field was located in the displaced, marginal, deprived, or normal zones defined in Fig. 1 (Fig. 4, B through E). One can see from the results that the magnitude of the shift in the auditory space map depends on the zone, indicating that vision can adjust different portions of the map differently (12). However, even in the portion of the map that was deprived of visual input (vision blocked by the spectacle frames), there was a significant tendency [analysis of variance (ANOVA); $P < 0.05$] for auditory best areas to be shifted in the direction predicted by the prismatic displacement, suggesting that shifts in one part of the map influence auditory spatial tuning in neighboring parts of the map, at least when there is no conflicting instructional signal. Such neighbor interactions across the map would help to prevent discontinuities in the map and would thus promote a continuous representation of space.

In this experiment, displacement of the visual field induced a dramatic abnormal shift in the auditory space map despite the

fact that all other potential sources of spatial information were unaffected by the prisms. Thus, vision dominates in the calibration of the neural map of auditory space, as it does in the calibration of sound localization behavior (13, 14). Under normal conditions, this powerful influence of vision would fine-tune the topography of the auditory map and align it precisely with the visual map.

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