(Fig. 2). Only three units had receptive fields that extended beyond ±50° in azimuth. In elevation, the centering appeared less restricted largely because of the elongate shapes of the receptive fields. Still, there was an unequivocal increase in the representation of auditory space around and just inferior to the intersection of the median and visual planes. (ii) The receptive fields of space-dependent units in each hemisphere demonstrated a strong contralateral bias with the greatest representation given to 0° to 20° contralateral (Fig. 2). Few fields extended farther than 15° ipsilateral. Thus the area of redundant representation in the left and right hemispheres was limited to ±15°, with the median plane receiving the greatest representation. (iii) Although there was a discernible tendency for space-dependent units from a single electrode track to have overlapping receptive fields, the trend was not strong enough to confirm a systematic representation of auditory space in field L.

Because the receptive fields of space-preferring units were poorly defined and expanded with increasing sound intensity, specific statements regarding their size and distribution are somewhat arbitrary. Nevertheless some generalizations can be made. Receptive field sizes of space-preferring units, measured at 10 db above threshold, tended to be large (typically greater than 40° in azimuth and 100° in elevation) although their preferred areas were often small (usually less than 30° in azimuth and 60° in elevation). The distribution of these receptive fields was similar to that of space-dependent receptive fields: primarily frontal with a strong contralateral bias.

The emphasis given by the owl's auditory system to the frontal area (±30° azimuth and +20° to −30° elevation) is not unlike that given by the visual system to the center of gaze: the number of units with receptive fields in this area is disproportionately large, and their fields tend to be small. Although the mechanism by which this "expansion of representation" is derived is necessarily different in these two sensory systems, the functional consequences may again be improved acuity and more detailed analysis of the stimulus. If so, then one would expect that the owl's spatial acuity for auditory stimuli would be maximal within the frontal area and would drop off rapidly as the sound source is located more peripherally, especially beyond ±50° in azimuth or elevation, where only units with large receptive fields are responsive.

Behavioral measurements have estimated the barn owl's auditory spatial acuity at less than 5° in both elevation and azimuth (*3–5*). Thus it is not surprising to find units with receptive fields that are restricted in elevation as well as in azimuth. However, the mechanism by which elevation tuning is achieved is less obvious than the binaural intensity or time cues that are likely to determine azimuthal tuning. Elevation sensitivity in mammals (particularly in man) is thought to be based on the elevation-dependent filter properties of the external ear (*11*). To be effective, such a mechanism demands both a wide-band noise stimulus and a broad range of frequency sensitivity. The owl, on the other hand, attains maximal spatial acuity when a target sound includes frequencies of only 5 to 9 khz and is quite accurate at localizing even a 7-khz pure tone (*4, 5*). Furthermore, although most of the units with small receptive fields were sensitive to noise bands, some were sensitive to tones and demonstrated marked elevation tuning when mapped with a tone burst stimulus. Clearly some other mechanism must be involved.

Elevation tuning in the barn owl might be achieved by comparing relative sound intensity at the two ears in the manner conceived for determining sound azimuth. Elevation-dependent intensity disparities result from a vertical asymmetry in the location of the owl's ears [the left ear is higher than the right ear (Fig. 1) (*3–5*)], the direction of maximum sensitivity for the right ear being 10° to 15° higher than that of the left ear (*12*). Thus, a binaural elevation cue is available to the owl. It remains to be shown, however, that this mechanism is the one responsible for the elevation tuning of single units.

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2. Space-dependent responses of auditory neurons have been demonstrated by using hand-held speakers [E. F. Evans, in *Ciba Foundation Symposium on Hearing Mechanisms in Vertebrates* (Churchill, London, 1968); A. R. A. Sovijärvi and J. Hyvärinen, *Brain Res.* **73**, 455 (1974)]. The existence of auditory receptive fields has been indicated by studies on multimodal neurons [B. G. Wickelgren, *Science* **173**, 69 (1971); F. Morrell, *Nature (London)* **238**, 44 (1972); U. C. Dräger and D. H. Hubel, *J. Neurophysiol.* **38**, 690 (1975)].
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6. By analogy to its connotation in contemporary visual research, the term "receptive field" will refer to the area of space within which a sound stimulus can influence the firing of an auditory unit.
7. A recording chamber was implanted over field L in each owl, an arrangement that allowed repeated recording over a period of 8 months.
8. The chamber was free of standing waves resulting from reflection; sound attenuation followed the inverse-square law throughout the length of the chamber.
9. Sound intensity was calibrated with a 2.5-cm condenser microphone (Bruel and Kjaer) at the position where the owl would be located. The frequency response of the 5-cm speaker was flat from 4 to 10 khz. Variations in sound intensity as a function of speaker location were less than ± 2 db except in a small area directly beneath the owl.
10. The highly pigmented pecten oculi in each eye, which is plainly visible ophthalmoscopically, provided a convenient landmark for aligning the owl's head. The visual plane is the horizontal plane containing the projection from each area centralis through the nodal point of the eye to the horizon. In the barn owl, the visual plane is located 8° to 10° below the plane containing the projections of the superior limbs of each pecten into space. The owl's visual plane was adjusted by monitoring the projection angle of the superior limbs of the pectens. The median plane was aligned by positioning the owl so that its pectens projected symmetrically on either side of the 0° azimuth plane.
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12. That the owl exploits this elevation-dependent intensity disparity is indicated by behavioral experiments in which one ear was plugged during sound localization. Under these conditions the owl commits consistent vertical errors (*5*).

13. We thank C. Adams for constructing the speaker carriage system, E. Akutagawa and G. Blasdel for technical assistance, and A. J. Hudspeth for critically reviewing the manuscript. This work was supported by an NIH postdoctoral fellowship (5 F32 NS 0552902) to E.I.K., an NSF grant (BMS 75-19180) to M.K., and a Spencer Foundation grant to J.D.P.

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Neoplastic Skin Lesions in Salamanders from a Sewage Lagoon Containing Perylene

Rose and Harshbarger (*1*) reported that tiger salamanders living in a sewage sedimentation lagoon had a high incidence of neoplastic skin lesions (including cancer) and suggested a chemical etiology for these neoplasms. In a search for a chemical agent, they reported 300 parts per million of perylene and a trace of benzopyrene (isomer not given) in this lagoon's sediment. They suggested that the source of perylene was related to jet aircraft activity on a nearby runway. We believe that this is not the correct source of perylene in this lagoon.

The presence of a single polycyclic aromatic hydrocarbon (PAH), rather than a complex mixture, usually indicates a natural source rather than anthropogenic input (*2*). In fact, high concentrations of perylene (and the absence of other PAH) have been reported for a number of sediments: Saanich Inlet, British Columbia (*3, 4*); Vema Fracture Zone (*4*); Santa Barbara Basin, California (*5*); Lake Biwa, Japan (*6*); Lake Washington, Washington (*7*); and the Amazon River (*8*). It is thought that perylene in these sediments results from the diagenesis of terrestrial pigments which have been rapidly deposited into a reducing sediment. This idea also seems to account for the presence of perylene in this sewage lagoon. We feel it is important not to perpetuate Rose and Harshbarger's suggestion that perylene in this lagoon results from the activity of jet aircraft when a natural source seems more likely.

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Windsor *et al.* offer another possible source of perylene for the sewage lagoon at Reese Air Force Base and suggest that the diagenesis of terrestrial pigments seems more likely. We offered four possibilities: a fuel spill, dumping (and subsequent removal) of asphalt into the lake, diesel fuel used as a mosquitocide, and jet exhaust. Recent conversations with the base entomologist confirmed what we had expected, that diesel fuel was used as a mosquitocide through 1976. The rate of application was 56 liters per acre. Since the lake is about 30 acres in area, the input is 1680 liters times two to five sprayings per year, or 3360 to 8400 liters per year. Agreed, this does not account for the disproportionately high level of perylene; however, recent evidence indicates that while perylene is high, other PAH's [notably benz(*a*)pyrene] are higher than originally reported. The absence of tumorous animals in other sewage lagoons not associated with the base (but not eliminated from the diagenesis of terrestrial pigments) further substantiates the view that the high lesion rate is base-related.

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Potassium Accumulation in Frog Muscle: The Association-Induction Hypothesis versus the Membrane Theory

Palmer and Gulati (*1*) demonstrated that frog muscle cells could accumulate K^+ up to a concentration of 580 m*M*, while accommodating Na^+ to a steady concentration of no more than 20 to 30 percent of that in the external medium. Since according to their calculations the muscle cells have less than 580 m*M* anionic sites, they concluded that (i) (intracellular) K^+ is free under all conditions; (ii) at most 20 percent of the cell water is bound, in the sense that it excludes electrolytes; and (iii) the data support the membrane theory, in which the cell is thought to represent a simple Donnan equilibrium, but refute the basic tenet of the association-induction hypothesis.

I criticize the report of Palmer and Gulati for two reasons. First, the version of the association-induction hypothesis which they present is incorrect, and hence their conclusions concerning it are invalid. Solute distribution in living cells has been described in a general equation (*2, 3*) which, as applied to the intracellular K^+ concentration in moles per liter of cell water, $[K^+]_{cw}$, may be written as

$$[K^+]_{cw} = q_{K(Cl)}[K^+]_{ex} + [K^+]^{I}_{ad} + [K^+]^{II}_{ad} + [K^+]^{III}_{ad} \qquad (1)$$

where $q_{K(Cl)}$ is the equilibrium distribution coefficient of K^+ (as chloride) between the cell water and the external medium (*4, 5*); $[K^+]_{ex}$ is the equilibrium external K^+ concentration; and the last three terms refer to K^+ adsorbed on three different types of adsorbing sites. Equation 1 hypothesizes a cell K^+ fraction, indicated by the first term on the right-hand side, which increases linearly with increases of external K^+ and is thus unsaturable. Therefore, cell K^+ cannot be a saturable function of external K^+. Yet Palmer and Gulati's argument against the association-induction hypothesis rests on their statement that it is a crucial prediction of the hypothesis "that the K content of the cell should be a saturable function of external K" (*1*).

Second, Palmer and Gulati ignored relevant experimental findings, including their own. The evidence they ignored includes (i) the finding that the degree of displacement of an accumulated cation such as K^+ depends on the nature and not merely on the valence of the displacing cation, in agreement with the association-induction hypothesis and not with the Donnan equilibrium theory (*6*), and (ii) the long-established finding that at external K^+ concentrations below 2.5 m*M* the cell undergoes a cooperative transition, shifting toward and approaching total displacement of cell K^+ by Na^+ at zero external K^+ (*2, 7–11*). In (*1*) they presented only the range of experimental data which indicates that at very low external K^+ concentrations the amount of cell K+ does not approach zero but instead levels off at a constant high value of 150 m*M*, as demanded by the Donnan membrane theory.

I will now demonstrate that the data presented by Palmer and Gulati (*1*), the data presented earlier by Gulati and Reisin (*10*), and our experimental data together confirm the general equation for solute distribution presented as part of the association-induction hypothesis (*2*).

Potassium in cell water. According to the association-induction hypothesis, cell water existing as polarized multilayers on certain extended polypeptide chains is not nonsolvent water in the sense that it does not dissolve any solute. Instead, different solutes have various solubilities in it because they have different standard free energies of distribution between cell water and water in the surrounding medium (*4, 5*). So far, there has been little direct experimental investigation of $q_{K(Cl)}$ in cell water. The *q* value of KCl in water in a silica gel is 0.77, whereas that for NaCl is only 0.51 (*12*). Similar values were obtained for the nitrate salts (*13*). Both sets of data show that the *q* value for K^+ in this model system tends to be significantly higher than that for Na^+.

The concentration of Na^+ in the cell water in Palmer and Gulati's experiment was about 20 m*M* at an external NaCl concentration of 91 m*M*, giving $q_{Na(Cl)} = 20/91 = 0.22$. In our experiments, the somewhat higher value of 0.29 was obtained. Thus, $q_{K(Cl)} = 0.5$ should be a reasonable value under the conditions of Palmer and Gulati's experiment. This value yielded the first component of the theoretical curve shown in Fig. 1 as the straight line labeled C.

Adsorbed potassium. According to the association-induction hypothesis, fixed anionic sites on cell proteins (for example, β- and γ-carboxyl groups) in normal cells not only provide preferential adsorption sites (type I sites) for K^+ but also help to maintain cell shape and volume by forming salt linkages with oppositely charged sites (such as imidazole, ε-amino, and guanidyl groups) on neighboring proteins within the cells (*14*). Salt