demonstrated dependent fields. Still, limited extended 00 receiving tendency (Fig. 1)
lapping peared fields intensity, specific arbitrary. Nevertheless muthand frontal dependent
vation). 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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References and Notes
1. For reviews of neurophysiological studies on sound localization, refer to S. D. Erukkal, Physiol. Rev. 52, 237 (1972); M. Konishi, in Recognition of Complex Acoustic Signals (Dahlem Konferenzen, Berlin, 1977).

2. Space-dependent responses of auditory neurons have been demonstrated in several field speakers [E. F. Evans, in Ciba Foundation Symposium on Hearing Mechanisms in Vertebrates (Churchill, London, 1968); R. A. So- vijärvi and J. Hyvärinen, Brain Res. 73, 455 (1974)]. The existence of auditory receptive fields has been indicated by studies on multidimensional neurons [B. G. Wickelgren, Science 173, 69 (1971); F. Morrell, Nature (London) 238, 44 (1972); U. C. Dräger and R. A. So- vijärvi, Nature (London) 238, 48 (1972)]. Nevertheless, it has been established that certain narrow bands of frequencies can be delineated in the same area of space as that of a single unit.


6. By analogy to its 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 I 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 Kjær) 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 pectoral 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.


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 those conditions the owl commits consistent vertical errors (5).

13. We thank C. Adams for constructing the speaker carriage system, E. Kitagawa and E. A. Akutagawa for technical assistance, and A. J. Hudspeth for critically reviewing the manuscript. This work was supported by an NIH postdoctoral fellowship (5 F32 NS 052902) to E.I.K., an NSF grant (BSM 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 benzoperylene (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, 720

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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 mM, 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 mM anionic sites, they concluded that (i) (intra-cellular) 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, \([K^+]_{\text{lw}}\), may be written as

\[
[K^+]_{\text{lw}} = q_{\text{KCl}}[K^+]_{\text{lw}} + [K^+]_{\text{la}} + [K^+]_{\text{la}} + (1)
\]

where \(q_{\text{KCl}}\) is the equilibrium distribution coefficient of K+ (as chloride) between the cell water and the external medium (4, 5); \([K^+]_{\text{lw}}\) 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 mM 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 (i) 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 mM, 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 (\(\Delta G\)). So far, there has been little direct experimental investigation of \(q_{\text{KCl}}\) in cell water. The \(q\) value of KCl in water 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 mM at an external NaCl concentration of 91 mM, giving \(q_{\text{NaCl}} = 20/91 = 0.22\). In our experiments, the somewhat higher value of 0.29 was obtained. Thus, \(q_{\text{KCl}} = 0.5\) should be a reasonable value under the conditions of Palmer and Gulati’s experiments. 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, \(\beta\)- and \(\gamma\)-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, \(\epsilon\)-amino, and guanidyl groups) on neighboring proteins within the cells (14). Salt
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