survival of *Hyla* in replicates with higher predator densities can be attributed in part to a reduction in interspecific competition corresponding to a predator-mediated reduction in the survival and density of *Scaphiopus* and *Bufo* (Table 1).

Differences in survival to metamorphosis among the species of anurans resulted in significant differences in tadpole guild composition at different levels of newt predation (Table 1). The reversal in guild composition shown in Fig. 1 resulted from the steadily decreasing survival of *Scaphiopus* and *Bufo* that accompanied increased newt density, while *Hyla* survival increased along the same direction of the predation gradient. Differential predation experiments conducted with these species in the laboratory have demonstrated that *Scaphiopus* and *Bufo* are relatively preferred prey of *Notophthalmus*, and this result may account for their relatively poorer survival at higher predator densities (*12*).

The above results demonstrate that predation and competition can interact to produce deterministic patterns of relative abundance in a guild of vertebrate prey. Furthermore, the outcome of interspecific competition among tadpoles in the absence of predators is not a reliable predictor of tadpole relative abundance when newts are added to the community. *Notophthalmus* can act as a keystone species (*13*) and prevent the virtual exclusion of competitively inferior species by reducing the survival and density of competitively superior anurans. Any general predictive theory of community ecology must consider the importance of biological interactions among and within trophic levels to account for these results. While descriptive studies of vertebrates may provide only questionable support for the importance of interspecific competition in the structuring of communities, results from controlled experiments can demonstrate that analogs of natural communities may be dramatically structured by interactions among competitors and their predators.

PETER J. MORIN

Department of Zoology,
Duke University,
Durham, North Carolina 27706

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7. *Notophthalmus* regularly preys on the eggs and larvae of amphibians [B. Walters, *J. Herpetol.* **9**, 267 (1975)].
8. A guild is a subset of species in a community that exploits similar resources in a similar manner [R. B. Root, *Ecol. Monogr.* **37**, 317 (1961)].
9. Proportions representing relative abundances were angularly transformed to satisfy assumptions of multivariate normality. This transformation also eliminates linear dependence among the original proportions. The multivariate analysis of variance simultaneously tested the null hypothesis of no newt density effect on the transformed relative abundances of the three anuran species. Newt density significantly altered overall tadpole guild composition, Wilks lambda = .170 with associated parameters $u = 3$, $v_h = 3$, and $v_e = 12$. Because the overall rejection of the null hypothesis is dependent on patterns of variance and covariance among the variables across all treatments, univariate standard errors are inappropriate for these data and are excluded in Fig. 1 to preclude their erroneous use in a posteriori comparisons among pairs of means [N. H. Timm, *Multivariate Analysis with Applications in Education and Psychology* (Wadsworth, Monterey, Calif., 1975)].
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11. The stepwise multiple regression was performed with the stepwise procedure of the Statistical Analysis System; only independent variables with regression coefficients significantly different from 0 at the $P = .05$ level were retained in the linear model [J. Barr, J. H. Goodnight, J. F. Sall, J. T. Helwig, *A User's Guide to SAS76* (SAS Institute Inc., Raleigh, N.C., 1976)]. The lack of correlation between *Hyla* density and the mean *Hyla* weight confirms that the exclusion of *Hyla* density from the linear model reflects the absence of negative intraspecific density dependence, rather than a regression artifact.
12. Individual *Notophthalmus* were allowed to feed for 2 hours in 7-liter aquariums containing 40 tadpoles of equal size. Twenty tadpoles of each of two anuran species were present in a given replicate aquarium. This protocol was repeated 15 times for each anuran species pair, and the frequency of tadpoles eaten over all replicates for a species pair was examined with a chi-squared statistic for evidence of nonrandom predation. Results for four pertinent species pairs were *Rana : Scaphiopus* (12 eaten : 132 eaten, $\chi^2 = 100$, $P = .001$), *Rana : Bufo* (27 : 82, $\chi^2 = 27.7$, $P = .001$), *Bufo : Scaphiopus* (27 : 87, $\chi^2 = 31.6$, $P = .001$), and *Rana : Hyla* (73 : 96, $\chi^2 = 3.2$, not significant).
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Auditory Intensity Discrimination After Selective Loss of Cochlear Outer Hair Cells

Abstract. *The contributions of the inner and outer hair cells of the mammalian cochlea to auditory intensity discrimination were evaluated in a combined behavioral-anatomical study of the guinea pig. Intensity difference thresholds were unchanged from baseline values after selective destruction of outer hair cells, suggesting that those cells are unnecessary for normal intensity discrimination.*

The two populations of auditory receptor cells, the inner and the outer hair cells, differ morphologically in several important respects (*1*, *2*). Neural innervation patterns of the two cell types also differ; outer hair cells receive only 5 percent of the afferent innervation of the cochlea, and inner hair cells receive the rest (*3*).

Although precise functions have been assigned to the two populations of visual receptor cells, the rods and the cones, comparatively little is known regarding the possible differential activity of the

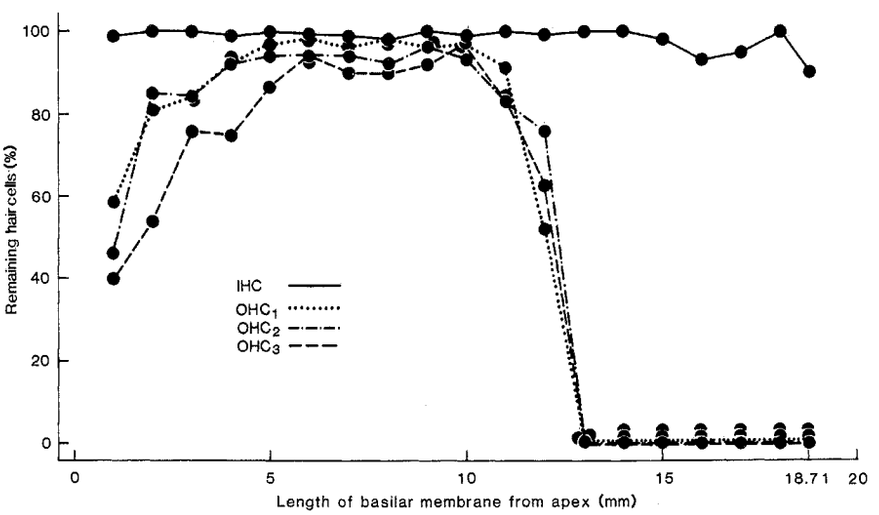

Fig. 1. Right ear cytocochleogram of S20.

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inner and outer hair cells. Behavioral experiments suggest that monkeys (*4*), guinea pigs (*5*), and chinchillas (*6*) are 40 to 60 dB less sensitive to pure-tone auditory stimuli after loss of the outer hair cells. Electrophysiological data (*7*) concur with these behavioral results, indicating that the outer cells are responsible for normal absolute auditory sensitivity. We now describe a combined behavioral and histological attempt to further distinguish activity of the two types by assessing intensity discrimination in the absence of the outer hair cells. Intensity difference limens (DL's) were defined as the minimum difference in intensity between two presentations of a pure tone reported reliably by the subjects. Our results suggest that the integrity of the outer hair cells is not necessary for intensity discrimination; subjects showed no change in DL's after destruction of the outer hair cells.

Three 3-month-old male albino guinea pigs (*Cavia porcellus*) were trained to report absolute thresholds (AT's) and DL's in a positive reinforcement operant conditioning procedure according to the psychophysical method of constant stimuli (*8*). Baseline AT's were determined for subjects S16, S17, and S20 at 2.0, 8.0, 16.0, and 32.0 kHz, and DL's at 2.0, 8.0, and 16.0 kHz for S16 and at 2.0 and 8.0 kHz for S17 and S20. DL's were measured at 20- and 70-dB sensation level (SL), that is, 20 and 70 dB above each subject's AT at each test frequency. AT's were considered stable when five successive determinations were within 10 dB at each test frequency; DL's were judged stable when the last five determinations were within 2 dB at each test frequency and SL. Threshold at each frequency was defined as that absolute intensity, or intensity difference, to which subjects responded 50 percent of the time and was determined by linear interpolation of the points bracketing 50 percent on psychometric functions. The mean DL before treatment at 70-dB SL was 3.2 dB.

After both AT and DL criteria had been satisfied simultaneously, subjects were subcutaneously injected with the aminoglycosidic antibiotic kanamycin sulfate (Kantrex) 100 mg per kilogram of body weight per day for 37 (S16), 38 (S17), and 63 (S20) days. The treatment selectively destroys a guinea pig's outer hair cells in the basal portions of the cochlea while leaving the corresponding inner hair cells relatively intact (*9*). Thresholds were measured throughout the period of kanamycin administration, and treatment was discontinued when the AT had shifted to 40 to 50 dB at 16.0 kHz (S16) or 8.0 kHz (S17 and S20). Thresholds were assessed until they had been stable for 4 weeks after treatment. Subjects were then killed and their cochleas prepared for microdissection and light microscopy (*10*). Cytocochleograms were constructed, in which the percentages of remaining inner and outer hair cells were plotted as a function of their position on the basilar membrane.

Table 1. Percentages of inner and outer hair cells remaining in the basal quarter (S16) or third (S17 and S20) of the cochlea of the better ear of each subject.

Subject	Hair cells remaining (%)	
	Outer	Inner
S16	4	76
S17	50	99
S20	2	97

The clearest results were seen in S20, for which the complete cytocochleogram for the right ear (Fig. 1) reveals that all three rows of outer hair cells were destroyed in the basal region of the cochlea, while the corresponding inner hair cells were still present. The left ear showed a similar pattern of hair cell loss. Condensed histological data from the cytocochleogram of the less impaired ear of each subject are shown in Table 1. Data of Prosen (*11*) has suggested that 8.0 kHz is encoded by receptor cells located one-third, and 16.0 kHz one-fourth of the total length of the basilar membrane from its basal end. Hence stimulus detection at 8.0 kHz for S20, and 16.0 kHz for S16, was probably mediated by inner hair cells.

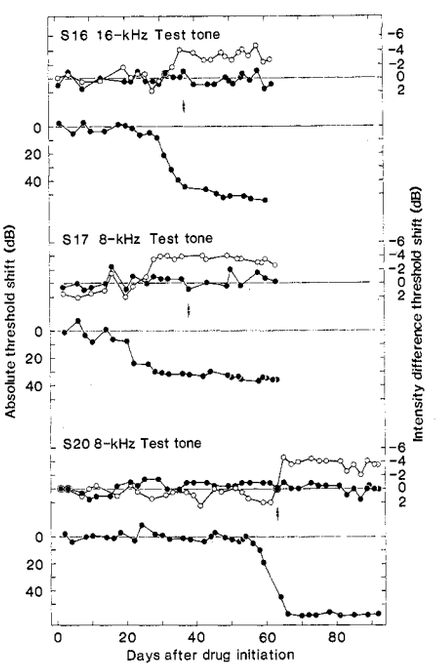

Fig. 2. Absolute threshold shift (lower filled circles) and intensity difference threshold shift, assessed at both a constant sound-pressure level (filled circles, upper part of each subject's data) and a constant sensation level (open circles), measured at the same frequency for each subject as a function of days after the drug treatment was initiated. Arrows indicate the termination of drug treatment for each subject.

Data of S17 are more difficult to interpret with regard to the contribution of the outer cells to detection of stimuli 8.0 kHz and above, since half of those cells were still present in the basal third of the cochlea. However, since 99 percent of the inner hair cells in this cochlear region were retained, any absolute threshold shift at high frequencies in S17 must have been the result of outer hair cell loss.

During drug treatment, all subjects suffered a 40- to 55-dB permanent hearing loss at the highest DL test frequency (Fig. 2). During the period of decline in absolute sensitivity to high frequencies, the sound-pressure level (SPL, re 0.0002 dyne/cm^2) of the standard stimulus in the DL test was changed daily to maintain a constant 20-dB SL; this level depended on the magnitude of the shift in AT measured at the test frequency on the previous day. Intensity DL's were determined at 20- and 70-dB SL before treatment; hence what was 70-dB SL for the normal cochlea became 20-dB SL for the kanamycin-damaged cochlea after a 50-dB permanent AT shift. Intensity DL's could therefore be compared at the same SL (20 dB SL) and the same SPL (the SPL equivalent to 70-dB SL for each subject) before and after kanamycin treatment and loss of outer hair cells (Fig. 2). Just as the AT increased by 40 to 55 dB at the highest DL test frequency, the DL at that frequency decreased by 3 to 4 dB when measured at an unchanging SL. When measured at a constant SPL throughout the same time course, however, no change in the DL accompanied the 40- to 55-dB AT shift at the same frequency.

DL's at the frequencies where no significant AT shift occurred—2.0 kHz for S17 and S20 and 2.0 and 8.0 kHz for S16—were unchanged when measured at a constant SL during that time course in which the DL at the highest test frequency decreased. Hence the apparent increase in sensitivity did not represent a change with extended training.

The histological data suggest that the high-frequency AT shift was a function of outer hair cell loss, since inner hair cells were 76 to 99 percent present in the basal portions of the cochleas of all subjects. Intensity discrimination was unaf-

fected at those frequencies, while absolute sensitivity declined by 40 to 55 dB; we therefore conclude that the outer hair cells are unnecessary for normal intensity discrimination. Although the precise mechanism of intensity discrimination is not clear, the results suggest that those processes contributing to the discrimination are unimpaired at high SPL's even though cochlear mechanics may conceivably be altered by outer hair cell loss.

Although the stereocilia of inner hair cells remaining after kanamycin treatment may not appear normal when examined by scanning and transmission electron microscopy (*12*), the DL's we measured must have depended on activity of the inner hair cells. To our knowledge this is the first demonstration that the outer cells are not necessary for auditory intensity discrimination. Although several investigators have indicated that normally hearing human subjects and those with a moderate sensorineural hearing loss have DL's of the same magnitude (*13*), patterns of hair cell loss in the hearing-impaired patients could only be inferred without histological confirmation.

The contribution of the outer hair cells to frequency discrimination and frequency selectivity is equivocal (*14*). Assessing all data regarding differential functions of the two types of hair cells, we conclude that the outer cells, essential for normal absolute sensitivity, are not necessary for at least one aspect of suprathreshold auditory signal detection—intensity discrimination.

CYNTHIA A. PROSEN*, D. B. MOODY
W. C. STEBBINS, J. E. HAWKINS, JR.
Departments of Otorhinolaryngology and Psychology and Kresge Hearing Research Institute, University of Michigan Medical School, Ann Arbor 48109

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* Present address: Auditory Research Laboratory, Northwestern University, Evanston, Ill. 60201.

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Reward-Induced Stereotypy: Modulation by the Hippocampus

Abstract. *In animals with hippocampal damage, the signaled administration of reward is sufficient to induce the sort of behavioral stereotypy and locomotion that heretofore has been observed only after drug administration. Haloperidol returns these behaviors to normal. The interaction of the hippocampus with reward helps to explain many well-known characteristics of animals with lesions in the hippocampus and may have relevance for catecholamine-based clinical disorders.*

Two of the most pervasive and probably least controversial features of the behavior of animals with extensive bilateral hippocampal lesions are excessiveness (*1, 2*) and invariability (*3, 4*). While these characteristics are sometimes exhibited in situations in which reward is not explicitly provided, they are especially visible when the brain-damaged animal is positively or negatively reinforced. Behavior established by these means is intense, rigid, and difficult to change (*2, 4*). An understanding of the interaction of the hippocampus with the dynamics of reward would help to explain much of the functional diversity that continues to be ascribed to the structure.

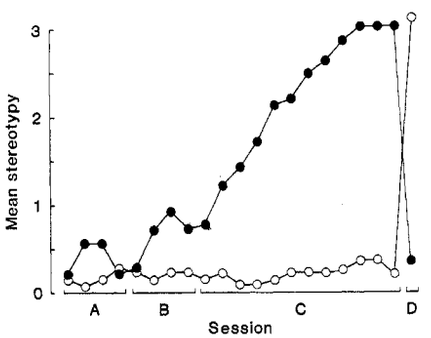

Fig. 1. Mean stereotypy scores of animals with hippocampal (closed circles) and neocortical (open circles) damage during free-fed (A), deprived (B), signaled reward (C), and drug (D) phases. Stereotypy scores: 0, asleep or stationary; 1, active; 2, predominately active but with bursts of stereotyped rearing and sniffing; 3, constant stereotyped activity over a wide area; and 4, constant stereotyped sniffing or head-bobbing in one place (6). Groups differed significantly in phase C [$F(1, 12) = 120.7$, $P < .001$]. Drugs affected both groups significantly [$t(6) = 13.0$ to 27.6, $P < .001$].

We now report that rats with extensive bilateral hippocampal damage display an exaggerated reaction to reward. This reaction consists of behavioral automatisms that bear a remarkable resemblance to the peculiar stereotyped and locomotor acts ("stereotypies") that follow *d*-amphetamine administration. Reward-induced stereotypy is returned to control levels by the administration of a catecholamine antagonist.

These findings were obtained from seven rats with bilateral lesions of the hippocampus and seven with aspiration ablations of the neocortex (*5*). The animals lived in clear polystyrene observation units equipped with movement transducers (phonograph cartridges with digitized outputs) that provided activity data. These data were recorded from 1300 to 1400 hours, the midpoint of the lights-on period. After two habituation days, the rater, who was unaware of the animals' surgical and drug conditions, entered the experimental room at 1300 hours daily and scored the degree of stereotypy as specified by a rating scale

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