of dimorphism through epigamic selection assume that offspring inherit attractive traits in Mendelian proportions (*17*). So, for example, one-quarter of all offspring of a male that is heterozygous for a dominant attractive allele with sex-limited expression displays the father's trait. However, if individuals are able to practice facultative sex ratio manipulation, a larger fraction of the progeny of attractive individuals will display the attractive trait and enjoy enhanced mate-getting abilities. One effect of this process should be that the rate of evolution of sexually selected traits is accelerated.

Patterns of sex ratio manipulation for attractiveness probably vary among mating systems and as a function of the genetics of inheritance of attractive traits. In promiscuous and moderately polygynous mating systems, females may benefit from biasing their offspring's sex as a reflection of their mate's attractiveness. In monogamous or somewhat polygamous mating systems, where males as well as females exert selectivity of mates, the attractiveness of both partners may be important, thus complicating the problem of optimal production. For example, while it may be relatively clear that an unattractive female mated to an attractive male should produce an excess of sons, it is less evident, a priori, what two attractive individuals should produce. If males' reproductive opportunities are more affected by attractiveness than are females', then (i) it may benefit females mated to attractive males to produce sons regardless of their own attractiveness, and (ii) it may be less advantageous for males to reproduce with attractive individuals. The latter possibility is supported by data indicating that attractive males have a reproductive advantage over other males, whereas attractive females have fewer offspring than females of intermediate attractiveness (Table 1). Under these circumstances selection for attractiveness in females should be more constrained, and female attractiveness should evolve more slowly.

These results indicate that birds can respond to novel nongenetic traits. Presumably they would display a similar capacity if mutations altered leg coloration or other aspects of species appearance. Thus by manipulating artificial indices of attractiveness, it would seem possible to investigate behavioral processes that affect the evolution of species traits.

NANCY BURLEY

Department of Ecology, Ethology, and Evolution, University of Illinois, Urbana 61801

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7. Data on 11 "white" birds are excluded because birds with this plumage mutation cannot be accurately sexed on the basis of external appearance. Data are also excluded for one homosexual female couple (orange-blue) that raised four clutches with no apparent male assistance.
8. From January on, the aviary contained offspring that were physiologically capable of reproduction. However, they were not observed to make nesting attempts during the interval for which data are reported here.
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15. Zebra finches are found in most parts of continental Australia and on some neighboring islands. They are excluded only from wet sclerophyll forest and rain forest [J. A. Keast, *Emu* **58**, 219 (1958)].
16. In captivity they have formed hybrids with at least 15 species [K. Immelmann, *Australian Birds in Bush and Aviary* (Halstead, Sydney, 1965)].
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18. I thank C. Coopersmith for assistance with data collection and the following people for advice: A. W. Ghent, S. Rohwer, R. Symanski, and M. F. Willson. Supported by the University of Illinois Research Board.

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Neural Correlates of a Nonjammable Electrolocation System

Abstract. *The detection of objects by the electrosensory system of weakly electric fish is subject to electrical interference such as that produced by the electric organ discharges emitted by neighboring electric fish. Most electric fish species have a behavioral reflex, the jamming avoidance response, which protects their electrolocation system against jamming.* Sternopygus *is unique in that it has no jamming avoidance response, yet can electrolocate even in the presence of jamming. It appears that* Sternopygus *protects electrolocation not by a behavioral strategy but by first-order central processing mechanisms that can distinguish between localized changes in the amplitudes of electric organ discharges caused by objects and large-field amplitude modulations caused by jamming. This mechanism acts as a local contrast detector and is functionally similar to the one used by retinal cells to respond to local contrast in light but not to overall changes in illumination.*

Weakly electric fish (Gymnotiformes and Mormyriformes) perceive objects in their immediate surroundings by emitting electric signals and evaluating small distortions of these signals as they are bent by objects. The emission of electric organ discharges (EOD's) generates an electric field around the animal. Electroreceptors, the primary sensory organs of the electrosensory system, detect objects as a local change in the amplitude of the electric field. Any extraneous signals that can distort the electric field (including EOD's emitted by a neighbor) can therefore alter the amplitude modulations caused by objects and "jam" electrolocation. Various behavioral modifications minimize this interference. The most studied is the jamming avoidance response (JAR), in which a fish shifts the frequency of its electrolocating signal to maximize the difference between it and the jamming frequency (*1*). Since the JAR protects an individual's electrolocation against interference by its neighbors, it is not surprising to find that it is a widespread behavior within the weakly electric fish. With the exception of the gymnotiform *Sternopygus*, all weakly electric fish so far tested demonstrate JAR's (*2*).

Behavioral experiments have shown that, even without JAR's, *Sternopygus* can electrolocate even in the presence of unnaturally strong jamming stimuli (*3*). In contrast, electrolocation in all other species tested, including the *Eigenmannia* spp. studied here for com-

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parison, is greatly impaired by jamming stimuli as weak as the near-field intensity of the animal's own EOD's. *Sternopygus* seems to have an alternative protection mechanism for its electrolocation system.

I now present the results of observations of neurophysiological responses to objects and the consequential effects of electric jamming on object detection. Comparative data recorded from the first-order electrosensory brain area, the posterior lateral line lobe (PLLL) of *Sternopygus* and of *Eigenmannia* show physiological responses that are direct neuronal correlates to the species-specific behavioral responses; for example, PLLL cells in *Sternopygus* respond to objects even in the presence of jamming, whereas responses to objects by the PLLL cells of *Eigenmannia* are obliterated by comparable jamming signals.

Sternopygus and *Eigenmannia* (*4*) were anesthetized and then lightly curarized with an intramuscular injection of Alloferin (*5*). Fish were held securely behind the pectoral fins with a small sponge-lined clamp. Aerated water flowed over the animal's gills through a glass tube inserted into the mouth. The tube also helped to stabilize the fish for recordings.

Because the synapses from the spinal motoneurons to the electric organ are cholinergic, curarization blocks EOD's. For this reason, an artificial EOD signal, *S1*, was provided through a pair of electrodes, one inserted through the mouth and into the stomach cavity of the fish, the other positioned near the tip of its tail (*6*, *7*). The artificial EOD signal matched (in both frequency and amplitude) the animal's EOD measured before the injection of Alloferin. A second stimulus, *S2*, applied transversely to the longitudinal axis of the fish was used to mimic the discharges of a nearby conspecific, and served as a large-field jamming signal. Under this type of jamming, the animal's entire lateral body surfaces are stimulated by *S2*. Both *S1* and *S2* were pure sinusoids. Measured independently near and perpendicular to the longitudinal axis of the fish, *S1* and *S2* were 0.5 mV/cm at 90 to 185 Hz and 1.5 mV/cm at 250 to 400 Hz for *Sternopygus* and *Eigenmannia*, respectively. The frequency of *S2* was set 2 Hz above that of *S1*, a frequency difference which has a detrimental effect on electrolocation of all species having JAR's (*3*).

An object, either aluminum or Plexiglas, 3.5 cm long by 1.4 cm wide, was moved by a servo system (*7*) parallel to and approximately 2.0 cm away from the longitudinal axis of the fish's body (Fig. 2) at a velocity of 3 cm/sec. Moving objects stimulate both electroreception (through distortions of the electric field of the fish) and the mechanoreception (through water displacements). However, physiological responses arising from these two modalities can be distinguished experimentally (*8*). Visual responses to moving objects were ex-

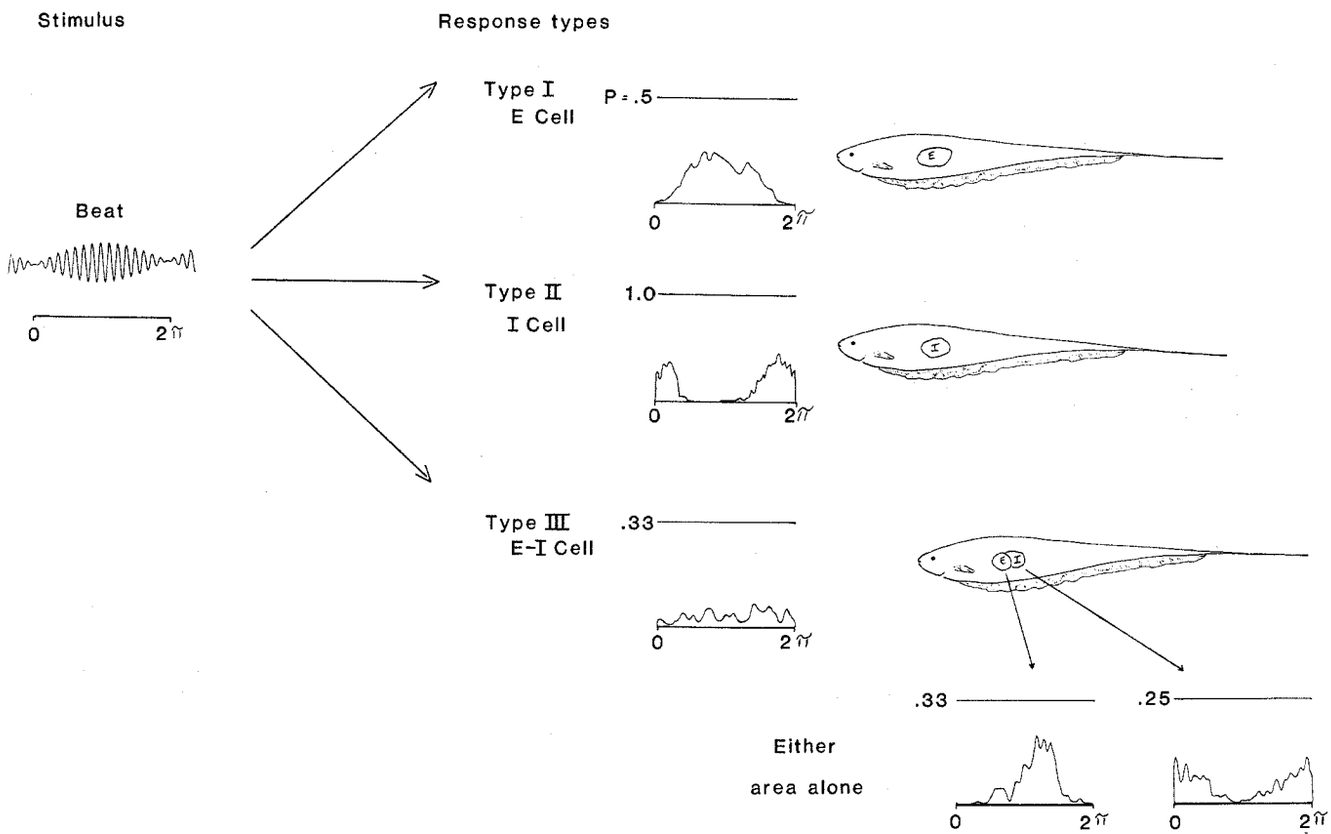

Fig. 1. Physiological cell types in the posterior lateral line lobe (PLLL) of *Sternopygus*. The stimulus is produced by the interactions between the experimental fish's EOD substitute, *S1*, and the large-field jamming signal, *S2*. Three types of cells can be distinguished. The excitatory (*E*) type I cells respond best to the maximum amplitude of the beat envelope (at π). The inhibitory (*I*) type II cells respond best to the minimum amplitude of the beat envelope (at 0 and 2π). Although both cell types are commonly encountered when recording from the PLLL of *Eigenmannia*, they are less abundant in the PLLL of *Sternopygus*, which contains many type III cells. The type III cells do not respond to large-field electric jamming signals. However, if *S2* is applied locally, such that the beating interactions between *S2* and *S1* stimulate only part of the receptive field, the cell responds. The receptive field of the type III cell shows a zone that responds near the maximum of the beat cycle and one that responds best to the minimum amplitude of the beat cycle. Upon stimulation of both zones, as during large-field jamming, the cell responds equally well to all phases of the beat cycle. Type III cells therefore are termed "beat-insensitive." Responses of single units, measured as the probability of firing on each *S1* cycle, is plotted against the phase of the beat cycle in radians. The difference in frequency between *S1* and *S2* is 2 Hz. The single units shown here were recorded from *Sternopygus*. Records for cell types I and II are qualitative representatives of the cells found in *Eigenmannia*.

cluded since fish were blindfolded during recordings (*9*).

All single-unit responses discussed here are from electroreceptive cells. Extracellular, single-unit recordings were obtained from the PLLL through the use of platinum-coated indium-filled glass pipettes (*10*). Responses of single cells were recorded in units of action-potential frequency as a function of the position of the object along the animal's body length or as a function of the phase of the beat cycle. Recording sites were marked by current lesions produced by the recording electrode or with horseradish peroxidase pressure injections (*11*).

The electric field surrounding an electric fish can be distorted by, for example, the bending of current lines by a nearby object or through interactions (beating) with the EOD's of a neighboring fish. One class of electroreceptive cells, the P units (probability coders), found in the PLLL of all wave-type gymnotiforms, is sensitive to the resulting changes in the amplitude associated with the electric field (*12*). In this study of the PLLL of *Sternopygus* and *Eigenmannia*, three types of P units were found: type I and type II (called E and I cells, respectively, in earlier publications) are found in the PLLL of both *Eigenmannia* and *Sternopygus* (*13*). These cells respond to changing amplitudes, either increasing (type I) or decreasing (type II) amplitude associated with the fish's electric field (Fig. 1) (*14*). They show no preference in beat frequency for all beat frequencies tested (ranging from 1 to 64 Hz). Since excitation by beat-related amplitude modulations masks their responses to objects, both cell types can be jammed (Fig. 2) (*15*).

The receptive field of the cell is the area of body surface that, when stimulated, produces a response in these cells. By applying voltages for *S2* through a pair of carbon-rod electrodes located 20 cm from either side of the fish, large-field jamming was produced. To map receptive fields, however, we need a localized jamming stimulus that interacts with *S1* over only a limited area (that is, smaller or equal to the size of the receptive field) of the fish's body surface (*16*). The receptive fields of types I and II cells were roughly 1 cm^2 each and were simple in that they consisted of an area that was either excited (type I) or inhibited (type II) by an increase in amplitude. In *Eigenmannia*, all of the units encountered in the PLLL were of these two types (N = 27). However, only a fifth (N = 46) of all PLLL units recorded in *Sternopygus* were of these two types. Four-fifths of the units encountered in *Sternopygus* were type III cells.

Type III cells have been recorded only in *Sternopygus* (*17*). Their receptive fields consist of two adjacent zones: one that shows an excitatory and one that shows an inhibitory response to increasing amplitude. If the animal's EOD is locally amplitude modulated, such that either the excitatory or the inhibitory zone is stimulated alone, the type III cells respond as if they were either a type I or a type II cell (Fig. 1, lower right). However, if both zones are stimulated together, for example during large-field jamming, they do not respond. Because of these characteristics, type III cells are able to respond to moving objects that cause independent, localized amplitude modulations to either zone alone even in the presence of large-field jamming stimulating both zones (Fig. 2).

The local circuitry responsible for the responses of the type III cells has not yet been determined. Two possible circuits for the inputs are suggested by the results from this study. (i) Type III cells may be third-order cells receiving converging inputs from types I and II (second-order cells). Since types I and II fire over broad ranges of the beat cycle (at the maximum or the minimum, respectively), simple addition of the two inputs would then produce a response with no preference for any part of the beat cycle, such as that shown for the type III cell (Fig. 1). Synaptic connections from types I and II onto type III cells should then be

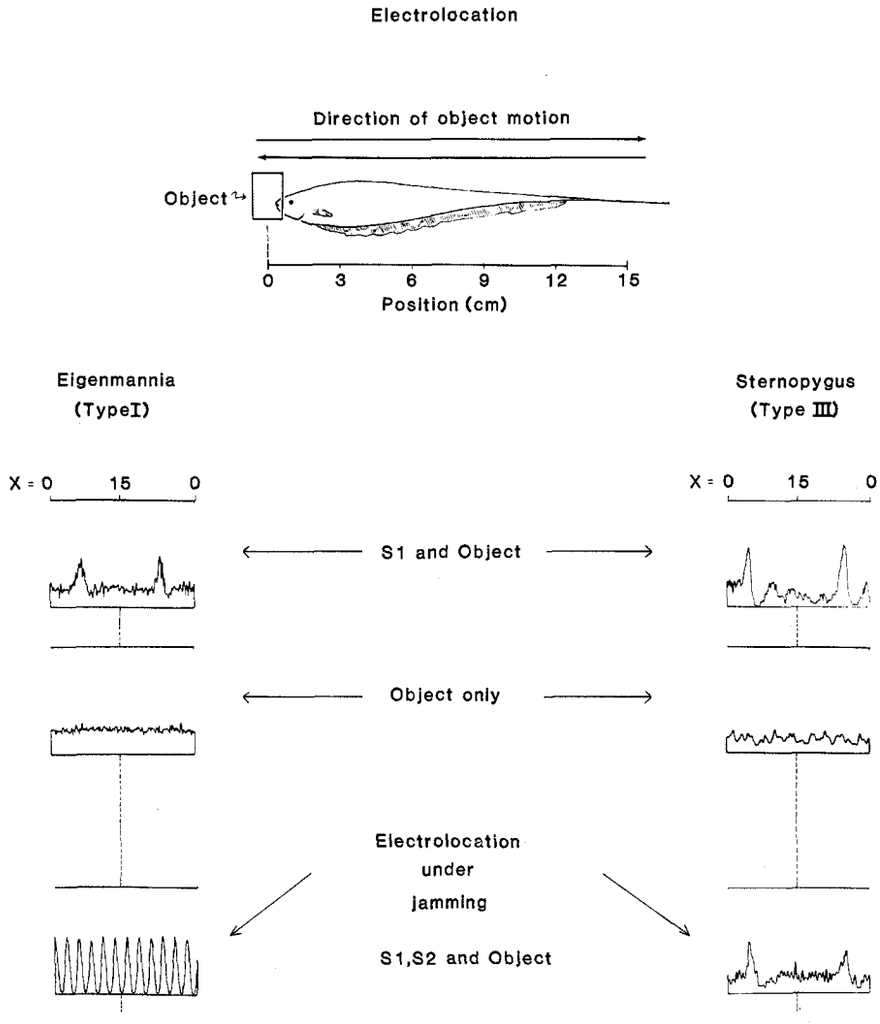

Fig. 2. The electrolocating responses to objects and the effects of jamming on object detection. Responses of single units, measured as the probability of firing on each *S1* cycle, are plotted against the position of the object relative to the animal's body length. The object, placed 2 cm to the side of the body of the fish, moves from its position near the head (X = 0) toward the tail (X = 15), reverses and approaches the head region again. All cell types show active electrolocation, that is, respond to objects only when *S1* is present. Since type I cells (left) are sensitive to amplitude modulations associated with beats (Fig. 1), responses to objects are masked when jamming signals are presented. Type III cells (right), because they are insensitive to amplitude modulations associated with large-field jamming (Fig. 1), respond to objects even in the presence of such jamming.

identical in sign. (ii) The behavior of the type III cells could also be attributed to a more generalized lateral inhibitory network consisting of an array of type I cells, all of which have neighboring receptive fields. In this case, the synaptic connections of neighboring type I cells onto type III cells should be opposite in sign.

From this preliminary study, as well as from detailed anatomical studies (*18*), many analogies can be drawn between the retina of the visual system and the PLLL of the electrosensory system. Functionally, both the ganglion cells of the retina and the type III cells of the PLLL are designed to respond maximally to local changes in the stimulus. Local contrast is accentuated, whereas uniform illumination or large-field amplitude modulations have little effect on the discharges of a ganglion cell or a type III cell, respectively.

JOANNE A. MATSUBARA
Scripps Institution of Oceanography, University of California at San Diego, La Jolla 92093

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3. J. Matsubara and W. Heiligenberg, *ibid.* **125**, 285 (1978).
4. *Eigenmannia virescens* (10 to 13 cm long) and two species of *Sternopygus—S. macrurus*, and an unidentified species characterized by a golden line running the length of the tail—(15 to 20 cm long) were studied. Fish were acclimatized to water conditions of *p*H 5 to 7, temperature 26° to 28°C, and resistivity of 10 kilohm-cm for at least 4 days before the experiments.
5. Hoffmann-La Roche Co. provided a sample of this drug.
6. The experimental set-up is illustrated in figure 1a of W. Heiligenberg, C. Baker, and J. Matsubara, [*J. Comp. Physiol.* **127**, 267 (1978)]. The artificial EOD signals, which were not phase-locked to the animal's pacemaker, seem to be sufficient for these studies for three reasons. (i) No known anatomical connections (efferent copy of the EOD) exist between the pacemaker and electrosensory processing areas (for example, posterior lateral line lobe or torus semicircularis) for *Sternopygus, Eigenmannia*, and *Hypopomus* (W. Heiligenberg, T. Finger, J. Matsubara, C. Carr, in preparation). In addition, these types of free-running artificial EOD signals are sufficient to drive behaviors such as the JAR in *Eigenmannia*, a closely related gymnotiform [Heiligenberg *et al.* (1978)]. (ii) The stimulus-field geometry produced by the stomach-tail electrode arrangement resembles that of the fish's natural EOD, as demonstrated by mapping isopotentials. However, the waveform of *S1* differs from that of the natural EOD in that it lacks the higher harmonic spectral frequencies. The fish may use these harmonic components of its natural EOD in texture (for example, capacitive) discrimination. (iii) The general features of electrolocation, such as encoding the type of object (conductive or insulative) are identical when using either *S1* or a natural EOD. This was observed by comparing the results from this study with results from studies that used the natural EOD's of *Apteronotus* (*7*).
7. J. Bastian, *J. Neurophysiol.* **38**, 285 (1975).
8. Since the objects were the same size, the mechanoreceptive cues were nearly identical, whereas, because of the differences in conductivity between the aluminum and Plexiglas, the electrical cues were not. Thus, the mechanoreceptive responses would be identical but the electroreceptive responses would be different. Moreover, there is no electroreceptive response to moving objects if the EOD substitute, *S1*, is removed.
9. Fish were blindfolded with a piece of black electrical tape fitted over the eyes and tied securely around the head.
10. K. Frank and M. Becker, in *Physical Techniques in Biological Research*, W. L. Nastuk, Ed. (Academic Press, New York, 1964), vol. 5, part A, p. 23.
11. For horseradish peroxidase (HRP) injections, the recording electrode was replaced with an HRP-filled glass pipette and lowered to the depth of the recording site.
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13. J. Bastian and W. Heiligenberg, *J. Comp. Physiol.* **136**, 135 (1980).
14. For square-wave amplitude-modulated *S1*'s, types I and II show adapting excitatory responses at the onset or offset, respectively, of the modulation.
15. H. Scheich, *J. Comp. Physiol.* **113**, 228 (1977).
16. The approximate center of the cell's receptive field can be identified by observing the location of the moving object during the maximum firing of the cell. "Local" jamming stimuli were then produced in this area. This was achieved by applying the voltage for the jamming signal through the left carbon rod electrode and a monopolar electrode placed 1 mm from the left side of the fish. The voltage was then decreased until the minimum voltage necessary for the cell to respond was attained (that is, until lowering the voltage any more produced no beat-related response from the cell). Keeping this minimum voltage constant, the monopolar electrode (which was always kept 1 mm from the body surface) was then moved systematically along the length of the fish until the cell's receptive field was defined.
17. P. Enger and T. Szabo [*J. Neurophysiol.* **28**, 800 (1965)] found directionally sensitive neurons in the PLLL of *Apteronotus*. These cells may be similar to type III cells in *Sternopygus*.
18. L. Maler, E. Sas, J. Rogers, in preparation.
19. Supported by NIMH grant PHSMH-2614904 and NSF grant BNS76-20761 to W.H. I thank W. Heiligenberg, T. Bullock, T. Platt, C. Baker, B. Kristan, B. Partridge, and two anonymous referees for their advice and criticisms during this study.

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Interaction Between Purine and Benzodiazepine: Inosine Reverses Diazepam-Induced Stimulation of Mouse Exploratory Behavior

Abstract. *Inosine, 2-deoxyinosine, and 2-deoxyguanosine completely reversed the increase in exploratory activity elicited in mice by diazepam. The inhibition of exploratory behavior by purines occurred at doses that when given alone have no effect on exploratory behavior. 7-Methylinosine, which does not bind to the brain benzodiazepine binding site in vitro, had no effect on the diazepam-induced increase in exploratory behavior. Behavioral effects produced by various combinations of inosine and diazepam indicate that the interaction between purine and benzodiazepine is antagonistic and support the hypothesis that the naturally occurring purines function in anxiety-related behaviors that respond to benzodiazepine treatment.*

The recent discovery of pharmacologically relevant, high-affinity, stereospecific binding sites for the benzodiazepines in the central nervous system (*1*) has prompted studies on the possible physiological significance of these sites and attempts at isolating endogenous ligands (*2*). Several naturally occurring inhibitors of the binding of ^{3}H-labeled diazepam have been isolated from mammalian brain and proposed as endogenous ligands (*3*). Our studies have focused on the purines inosine and hypoxanthine and on the structurally related 2-deoxypurines (*4*). Although these compounds are relatively weak competitive inhibitors of [^{3}H]diazepam binding in vitro, they appear to exist in the brain in high concentrations (*5*) that increase severalfold when brain slices are subjected to depolarizing stimuli (*6*).

The major actions of the benzodiazepines include anticonvulsant, muscle relaxant, and anxiety-reducing effects (*7*). A putative endogenous ligand must demonstrate pharmacological, neurophysiological, and behavioral properties similar to those of the benzodiazepines. Large doses of purines antagonize pentylenetetrazole-induced seizures in mice in a dose-dependent manner (*8*). Inosine applied by microiontophoresis or pressure injection to cultured mouse spinal cord neurons elicited a rapidly desensitizing excitatory response that showed cross-desensitization with benzodiazepines and a nondesensitizing inhibitory response that was blocked by benzodiazepines (*9*). Inosine antagonized the γ-aminobutyric acid (GABA)-mimetic action of diazepam in a model system in which electrical stimulation of the globus pallidus caused head turning in rats (*10*). These lines of evidence support the view that purines have a functional role in benzodiazepine-mediated actions. Since the most specific and clinically applicable property of the benzodiazepines is their anxiety-reducing effect, a putative endogenous ligand for the brain benzodiazepine binding site should provide some measure of anxiolytic action. We have developed a simple, automated, one-parameter test for the behavioral effects of benzodiazepines in mice (*11*) and now report that the purines completely block the behavioral changes produced by diazepam at doses which by themselves do not affect these behaviors.

The test depends on the natural tendency of mice to explore a novel environment, but to avoid a brightly lighted open

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