reduction in the male capture in the male-plus-female-baited traps was caused by a male-to-male inhibitory pheromone that interfered in some way with the normal approach response of males to females that were releasing sex pheromone (*14*).

Interactions among male moths probably occur only at those times when two or more males approach and attempt to copulate with the same female simultaneously. Thus, the biological significance of this male-produced pheromone might be associated with the increased reproductive efficiency that results when multiple males are prevented from competing for a single female.

Electrophysiological evidence indicates that males of a variety of noctuid species may be able to sense their own scent-brush odors (*1*, *4*, *15*). Whether such scents could be dispensed into the air of fields containing males and females of certain pest lepidopterous species, so as to prevent mating and thus provide a selective means of pest control, remains to be determined.

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5. In other experiments (unpublished), we have found that either an extract of the anterior abdominal scent brushes of male *P. unipuncta* or synthetic benzaldehyde also cause an inhibition of the precopulatory behavior exhibited by males in response to pheromone-releasing females.
6. The colony was maintained by a method similar to that described by H. H. Shorey and R. L. Hale [*J. Econ. Entomol.* **58**, 522 (1965)]. All stages were held at 25° ± 2°C, under a photoperiod of 12 hours of light and 12 hours of darkness.
7. A red light provided illumination in the experimental room. The light intensity was measured with a Photovolt photometer, model 200M. Observation was also aided by occasional use of a dim red flashlight.
8. The cylindrical tunnel measured 7 cm (inside diameter) by 100 cm, and each cage, which tightly fit in the tunnel, measured 6.5 cm (diameter) by 8.5 cm. Air velocity in the tunnel was maintained at 25 cm/sec.
9. Two types of response, characteristic for sex pheromone-stimulated male moths, were measured, namely, wing fanning and attempted copulations. Because no females were present in the male cages, copulatory attempts were directed from one male toward another. These responses were measured at 15 and 60 seconds after the female cage was placed in the tunnel, and the percentage of response for any one cage was calculated as follows:

$$\frac{N_1 + N_2 - 2B}{2(N_0 - B)} \times 100$$

where N_0 is the number of males in the cage, N_1 and N_2 are numbers responding after 15 and 60 seconds, respectively, and B is background number responding immediately before stimulation.
10. For the 10,10,10,5,5,5,5-male sequence, 26 replicates (separate stimulations) were conducted over 5 days, and for the 0,0,0,5,5,5,5 sequence, 20 replicates were conducted over 4 days. All moths used in this and other experiments were 3 to 6 days old.
11. Numbers of observed behaviors in the first three consecutive cages were 10,10,6, and in the last three were 5,2,1.
12. During the experiment, the numbers of females with pheromone glands extruded and maintaining the typical receptive posture were 26 and 41 in the upwind and downwind cages, respectively. This lack of inhibition of female pheromone-releasing behavior by male scent was seen in an experiment, in which seven cages containing four males or four females each were placed in the tunnel, starting with a female cage and with sexes then alternating downwind. During 21 different 2-minute observation periods conducted over three nights, the percentages of females observed in the typical receptive posture were 39 ± 6 (standard error); 57 ± 6; 45 ± 7; and 52 ± 8 from the most upwind to the most downwind cage. In addition, we have observed that antennectomized females accept males in copulation as readily as do females having intact antennae.
13. Double cone traps, identical to those described by R. K. Sharma, H. H. Shorey, and L. K. Gaston [*J. Econ. Entomol.* **64**, 361 (1971)], were supported at 1-m elevation in the field. During three of the nine experimental nights, two traps of each type were placed in the field. The minimum distance between the traps was 20 m. Positions of the traps were changed at random nightly, and the females were replaced once during the experiment. The female enclosure was a 5 cm (diameter) by 12 cm wire-screen cage, and the male enclosure was a 8.5 cm (diameter) by 12 cm cage. Female and male enclosures were provided with 10 percent sucrose solutions.
14. C. J. Sanders [*Can. Entomol.* **110**, 43 (1978)] has reported that sex attractant traps for the male spruce budworms, *Choristoneura fumiferana* (Clem.) have a reduction in attractancy over time, apparently because the odor of males initially trapped repels other males.
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Echo Detection and Target-Ranging Neurons in the Auditory System of the Bat *Eptesicus fuscus*

Abstract. *Some of the neurons in the nucleus intercollicularis and auditory cortex of the echolocating bat* Eptesicus fuscus *respond selectively to sonar echoes occurring with specific echo delays or pulse-echo intervals. They do not respond for a wide range of other types of sounds or for sonar echoes at longer or shorter pulse-echo intervals; they may, therefore, be specialized for detection and ranging of sonar targets.*

We have made single-unit recordings from the auditory cortex, inferior colliculus, and nucleus intercollicularis in lightly anesthetized bats of the species *Eptesicus fuscus* (big brown bat, Vespertilionidae). These bats orient themselves and seek prey by echolocation. The responses of neurons were studied with pairs of acoustic stimuli simulating sonar sounds and echoes, and several types of response patterns were observed. Some of these neurons responded exclusively to echoes following more intense pulses and then only when the echo time delay or pulse-echo interval was within a restricted range. These units exhibited properties that were expected from knowledge of echolocation behavior and the acuity of target range (echo time delay) perception by bats (*1*).

Each bat was initially anesthetized with sodium pentobarbital (25 mg per kilogram of body weight). The top of the skull was exposed and dried, the head of a small nail was glued to the skull with acrylic adhesive (Eastman 910) and dental cement, and a small hole was made through the skull to insert a recording electrode. The bat was placed in a Plexiglas holder, which was suspended from an aluminum rod with a rubber band to absorb mechanical stress from the bat's movements, and the bat's head was rigidly held by clamping the attached nail to another aluminum rod. Both rods were mounted on a small steel platform used for supporting the preparation. The bat and the platform were placed in a soundproof room at 34°C for 3 to 4 hours before physiological recordings were begun. Generally, the bat's eyes were open, and pinching a leg elicited a withdrawal reflex, indicating that the bat was lightly anesthetized or awake. Either a tungsten microelectrode (tip diameter 2 to 5 μm) insulated with Insl-X, or a 3*M* KCl-filled glass micropipette (tip broken to about 1 μm diameter) was then lowered onto the surface of the brain overlying the desired recording site. Subsequent advance of the electrode into brain tissue was controlled from outside the soundproof room with a calibrated hydraulic microdrive. The stability of

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this preparation frequently permitted recording from a single neuron for as long as 2 to 3 hours.

Acoustic stimuli consisting of pure-tone bursts or frequency-modulated (FM) bursts were presented singly or in pairs to simulate the bat's own echolocation sounds and echoes. Sounds were delivered with varying intensities and time intervals through an electrostatic loudspeaker (*2*) placed 18.5 cm away from the bat's left ear, which was contralateral to the recording site (right hemisphere). The stimuli used to search for units as the electrode was advanced were sequences of pulse-echo pairs with the echo 20 dB weaker than the initial pulse. These signals were three-harmonic FM bursts 1.6 msec in duration with the first harmonic sweeping linearly downward from 60 to 23 kHz. The sounds had a nearly uniform (± 3 dB) power spectrum from 23 to 90 kHz and were similar to orientation sounds used by *Eptesicus* (Fig. 1). The repetition rate of the pulse-echo pairs and the pulse-echo time interval or echo delay were varied to simulate the series of sounds that might be heard by a bat while detecting and pursuing prey or approaching an obstacle (*3*) (Fig. 1c). Only neurons responding to these biologically relevant search stimuli are reported here.

Neural responses and acoustic stimuli were recorded on an instrumentation tape recorder (Lockheed Store-4D) and analyzed subsequently with a computer (PDP-11/40) or a storage oscilloscope. The bat was killed after 1 or 2 days of recording sessions, and the electrode tracks in brain tissue were identified histologically.

Three classes of neurons and neural response patterns were observed. Members of the first class responded to pulse-echo pairs at certain intensities, but their responses appeared to be a consequence of responsiveness to the pulses alone. Most of these neurons responded to individual FM bursts only when they were separated by rather long time intervals, and they were characterized as having long recovery cycles. Nevertheless, a number of these neurons, particularly in the nucleus intercollicularis, responded to both the pulse and the echo if the echo intensity was sufficiently large and the pulse-echo interval sufficiently long. These particular neurons exhibited low-intensity thresholds, near the behavioral thresholds for *Eptesicus* (*4*). Their occasional response to echoes reflected their general sensitivity and recovery from a refractory state and was not a response to the "pairness" of pulses and echoes as such.

Neurons in class 2 also responded to individual FM bursts. In the presence of a weaker echo this response was suppressed in some cases for short pulse-echo intervals (<10 msec) and in other cases for long pulse-echo intervals (> 20 msec). The range of pulse-echo intervals for which suppression of the response to the pulse occurred varied from neuron to neuron and was sometimes small.

The neurons of class 3 are interesting because they responded to the paired nature of the pulses and echoes and because they responded selectively to a restricted range of pulse-echo intervals or echo delays (*5*). These neurons never responded to a single pure-tone or FM burst, regardless of intensity, but responded reliably to pulse-echo "pairs" over a wide range of intensities when the pulse-echo interval fell within a particular range. Figure 2 (a to d) shows histograms representing responses of one of these echo-sensitive neurons located in the intercollicular nucleus. This neuron was silent unless stimulated by appropriate pulse-echo pairs, never firing spontaneously or to individual sounds during our observations. The presence of an echo 7 to 15 msec after the pulse always led to one or two spikes about 8 msec after the echo (Fig. 2e). Changes in relative echo amplitude did not much influence the range of pulse-echo delays characteristic of the neuron (Fig. 2, a to c), but the delay range shifted slightly when the pulse's absolute amplitude changed (Fig. 2, b and d). High echo amplitudes generally led to reduced responsiveness (Fig. 2a). Data in Fig. 2 were obtained with the search stimulus sequence (Fig. 1c); the separate manual control of pulse repetition rate and echo delay indicated that pulse-echo delay determined the selectivity of the neuron's response, but the repetition rate of the pair or the sequence of presentation of different echo delays did not. These neurons all responded to the echo, but the responses were conditioned by the presence of the pulse at a specific range of earlier times.

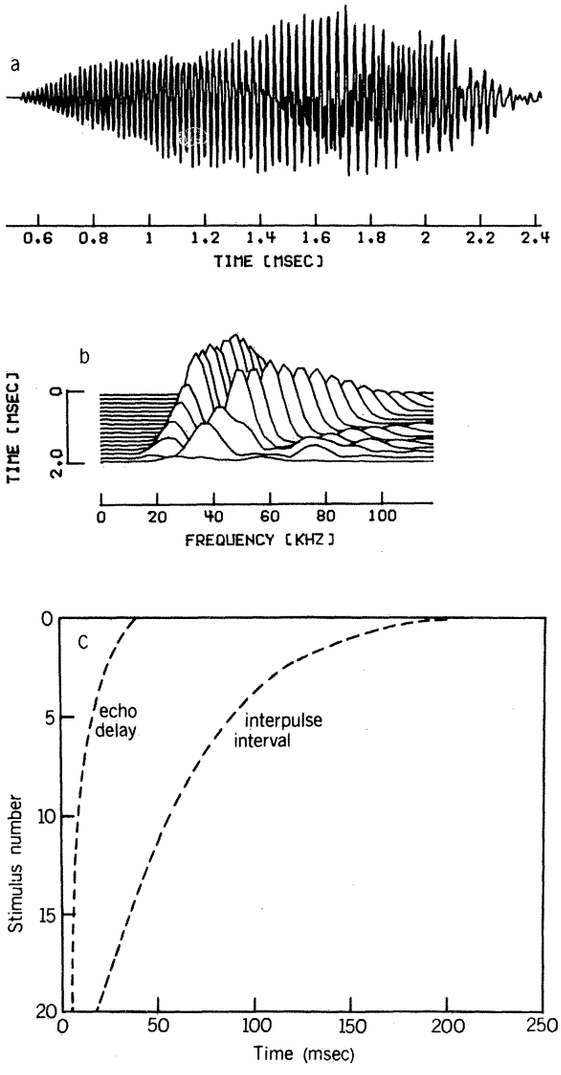


Fig. 1. The waveform (a) and time-frequency structure (b) of the simulated *Eptesicus* sonar sound used as a stimulus to search for neurons and to study responses of neurons. Such sounds were presented in pairs, using time intervals within and between pairs that simulated the sequence of sounds encountered by a bat approaching a sonar target as shown in (c). The graph showing pulse-echo intervals or echo delays and interpulse intervals is to be read in successive horizontal sections from the top down. Beginning at the top left, the first pulse occurs at zero time, followed by its echo (20 dB weaker) at 40-msec delay and then by the second pulse at 200 msec. Both the echo delay and the interpulse interval shorten as succeeding stimuli take place, corresponding to the progressive shortening of target range and the bat's increase in pulse emission rate as the target gets closer. Only neurons responding to such sequences of search stimuli are described here. There are 20 pairs of pulses and echoes in each search sequence.

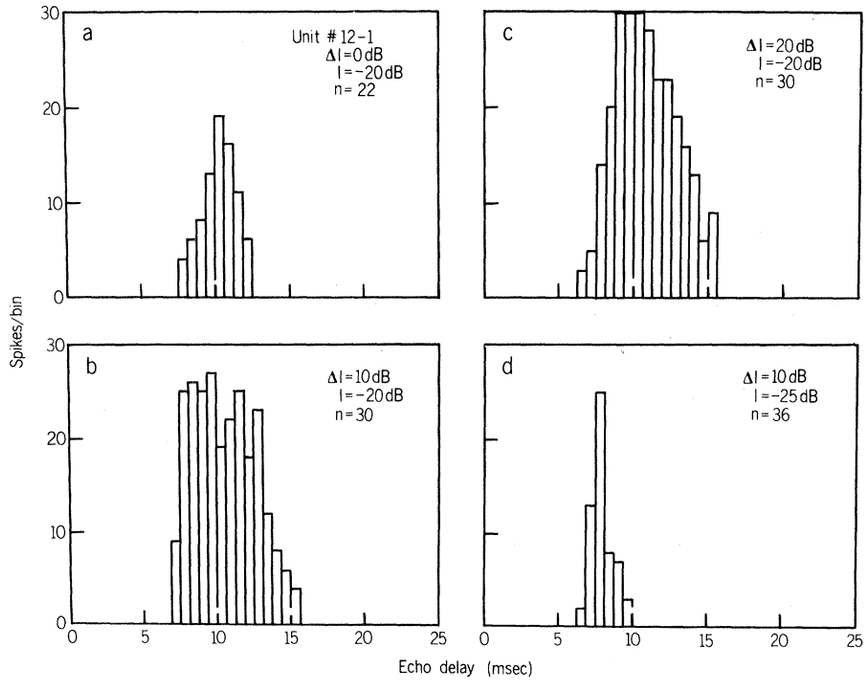
The "paired" character of the pulses and echoes was a feature required to discharge neurons in the third class, and the units were "tuned" to particular ranges of pulse-echo delays, different from one neuron to another. The responses of these neurons suggests that echo delay, the acoustic cue for target range to the bat (*1*), is processed in the time domain (*6*), and that some of the neurons involved may also respond exclusively to echoes. These results additionally suggest that bats may not need an efferent copy of their sonar emissions to determine range; the directly heard sonar sounds may constitute an afferent signal as reference for processing of echoes to determine target distance. The location of these neurons in the intercollicularis nucleus is not surprising. Spatial information associated with visually, tactually, and acoustically guided behavior is represented in the midbrain (*7*), and target range is a spatial feature that is important to echolocating bats.

Some neurons in the auditory cortex also responded selectively to echoes at certain pulse-echo intervals. However, cortical neurons in our sample were more difficult to study because they responded infrequently. In contrast, those neurons in the intercollicular nucleus fired for every appropriate pulse-echo pair. Firing preferences for certain pulse-echo delays were observed at ranges from 4.5 to 20 msec in different neurons, corresponding to targets at ranges from 0.75 to 3.5 m. Target range may thus be encoded by a neural "place" mechanism incorporating different delay-tuned neurons in the central nervous system, presumably at levels above the inferior colliculus. We have searched for this type of neuron in the inferior colliculus, but all neurons encountered were of class 1 or class 2, and none exhibited selective responses to pulse-echo delays. Rather, they tended to respond to both the pulse and weaker echoes at a wide range of delays.

Neurons of class 3 that occur in the intercollicular nucleus and auditory cortex clearly differed from neurons located in the inferior colliculus that have been described previously (*8*). Neurons in the inferior colliculus respond precisely to the timing of stimuli and may exhibit some sensitivity to echoes as a consequence of recovery cycles, but they do not show the rigid response to paired stimuli at certain pulse-echo delays that characterizes class 3 neurons here. It is possible that the neurons described previously and perhaps class 2 neurons in our sample are prerequisite to the selectivity to echoes, to tuning to pulse-echo time intervals, and to the precision in firing latency shown by class 3 neurons.

The neurons of class 3 unambiguously extracted echoes at certain delays as features of acoustic stimuli that are of biological relevance to bats. They are among the more sophisticated feature-detecting neurons yet described in the auditory system. We have used artificial sounds, the bat's echolocating pulse, and echoes in a simulation that differs from the normal situation in that the first pulse is not generated by the bat. It is conceivable that the sensitivity of the neurons we have studied would be altered by the active emission of orientation sounds, as has been demonstrated previously (*9*). It would be interesting to study the neural responses in behaving bats when they actually emit echolocating pulses to hunt.

Hearing is a sense superbly capable of small temporal discriminations, for example, in sound localization and in perception of periodicity phenomena (*10*). The preservation of time information in sounds as they are processed in the peripheral and central auditory system is well documented at the single-unit level (*8*, *11*), but few data exist on the neural encoding of temporal information as distinct from preservation. The neurons described in class 3 here may reveal something about the neural basis for perception of temporal aspects of sounds. The clear behavioral significance of



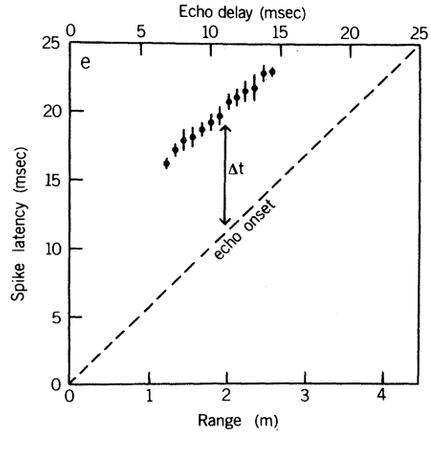


Fig. 2. Histograms of responses of a neuron in the nucleus intercollicularis to search stimuli simulating approach to a target (a to d). This neuron always responded with a latency of about 8 ± 0.15 msec after the echo (e). The unit required a pair of stimuli separated by 7 to 15 msec for a response to occur. Stimulus intensity is expressed as dB re 10 N/m^2, approximately the intensity of the emitted orientation sound of the bat. Pulse intensity, $I = -20$ dB, corresponds to the intensity of the emitted pulse as the bat hears it, and ΔI is the further attenuation of the echo below the level of the initial pulse. Note that decreasing echo strength relative to pulse strength increases the unit's response to the pair of sounds here (a to c). In these histograms n is the number of repetitions of the entire search stimulus sequence (Fig. 1c) used to assemble the data shown. Changing pulse absolute intensity sometimes affected the echo delay tuning of the neuron slightly (d). The unit responded with a constant latency (Δt) after the echo (e) and appeared to be locked to the echo, but conditioned by the requirement that the pulse occur 7 to 15 msec earlier. The unit responded to every echo with one or two spikes per echo when the echo delay was appropriate and was otherwise not active at all. This neuron responded to echo delays corresponding to target ranges of 1.2 to 2.6 m. Graph (e) shows the data of histogram (c).

pulse-echo intervals in orientation by bats makes this example a good illustration of the use of temporal information, and the neurons observed here may eventually lead to detailed knowledge of further neural mechanisms in echolocation. The role of these neurons within the totality of the bat's auditory system is not known from our data.

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Hamster Refractoriness: The Role of Insensitivity of Pineal Target Tissues

Abstract. *Hamsters exposed to short days undergo gonadal collapse followed by recrudescence and insensitivity to the regressive effects of such photoperiods. This refractoriness may be due to exhaustion of the pineal gland or desensitization of its target. Hamsters whose gonads had spontaneously recrudesced were injected with melatonin (25 micrograms per injection) once daily (known to induce regression in intact hamsters) or thrice daily (reported to arrest reproduction in pinealectomized hamsters) for 7 weeks. In neither case did refractory hamsters respond to melatonin treatment. The gonads of intact hamsters treated with melatonin for 21 weeks regressed and spontaneously recrudesced along a normal time course. These results indicate that gonadal refractoriness is due to insensitivity of the target tissues of the pineal gland and imply that melatonin participates in photoperiodic regulation of reproduction in the golden hamster.*

The seasonal breeding cycles of many vertebrates include a period of refractoriness to stimuli that induce gonadal regression at other phases (*1*). Photoperiods of less than 12.5 hours of light per day induce reproductive quiescence in the Syrian golden hamster, *Mesocricetus auratus* (*2*). Either pinealectomy or exposure to long days accelerates recovery of reproductive competence in hamsters whose gonads have regressed, but even the gonads of hamsters maintained on short-day photoperiods recrudesce spontaneously (*3*). Such spontaneous regrowth is thought to account for the return of reproductive activity in nature (*4*).

Hamsters whose testes have recrudesced remain insensitive to the regressive effects of short photoperiods unless they are exposed to at least 10 weeks of long days (*5*). Two alternatives have been offered to account for refractoriness to short days: (i) termination of production of the pineal gland's antigonadal factor (pineal exhaustion hypothesis) or (ii) desensitization of the pineal's target tissues (presumably in the brain) to its hormone (target insensitivity hypothesis) (*4*).

Melatonin, an indole whose rhythmic synthesis is largely restricted to the pineal, has been implicated in photoperiodically induced gonadal regression in both sexes. Daily injections of 10 or 25 μg of melatonin shortly before the end of the light phase induce testicular regression and arrest of the estrous cycle within 7 weeks in intact hamsters maintained in 14-hour photoperiods (LD 14:10) (*6*). Pinealectomized animals are unresponsive to such treatment. Three daily injections of melatonin at 3-hour intervals beginning 4 hours after the onset of light induce testicular regression in pinealectomized but not in intact animals. These differences in sensitivity of intact and pinealectomized hamsters may reflect an interaction between endogenous and exogenous melatonin or a role of the pineal in phasing the responsiveness of target tissues to pineal hormones (*6*).

In the experiments described here I exploited the differences in responsiveness of intact and pinealectomized hamsters to exogenous melatonin in order to determine the etiology of postregression testicular refractoriness. If pineal exhaustion accounts for the insensitivity of the testes to short days, refractory hamsters should be functionally pinealectomized and therefore induced to regress only by thrice daily injections of melatonin. If refractoriness results from insensitivity of target tissues to pineal hormones, such animals should be unresponsive to exogenous melatonin regardless of the timing of its administration. The target insensitivity hypothesis further predicts that the gonads of hamsters induced to regress by melatonin treatments will recrudesce if such injections are continued for several additional weeks. Such an outcome would also imply that spontaneous recrudescence results from the same physiological change responsible for testicular refractoriness. The results of the experiments indicate that the pineal's target tissues do become insensitive to the action of its antigonadal hormone.

Sexually mature male golden hamsters (LAK-LVG) were purchased from the Lakeview hamster colony (Newfield, N.J.) or were bred in our laboratory from similar stock. Animals were housed in groups and maintained under conditions of LD 14:10 (lights on at 0700 hours) prior to experimental use; they were caged singly thereafter (*7*). Testicular condition was monitored by periodic laparotomies (*8*).

Experimental hamsters (N = 44) were laparotomized and divided into two groups matched for body weight and testis index. After an interval of 47 days, one group was transferred to a photoperiod of LD 10:14 (lights on at 1000 hours) while the other was placed in constant darkness (*9*). Laparotomies performed 39 and 210 days later documented regression and spontaneous testicular recru-

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