as defined by the null criterion was also considered selective according to the statistical measure. Thus the two categories are not mutually exclusive.

14. Tiao and Blakemore (*12*) using the "null" criterion reported that about 12 percent of the cells in the hamster's superior colliculus were directionally selective and that these cells appeared to occur in clusters. In this regard, it should be noted that in nine of the 14 strobe-reared hamsters we tested no "null" cells were encountered. The minimum number of cells tested in any of these animals was five. In the normal ($N = 17$) and dark-reared ($N = 12$) hamsters in which at least five cells were tested for directional selectivity, there was only one case (a dark-reared animal) in which a "null" cell was not encountered. The findings argue against the possibility that the reduced incidence of directionally selective cells observed in the strobe-reared hamsters resulted from sampling error. The reasons for the difference between our estimate for the percentage of "null" cells in normal animals and that provided by Tiao and Blakemore (*12*) are unclear, but there may have been differences in the anesthetic agents used or in the sampling characteristics of the microelectrodes employed. These variables were maintained constant for each group of animals investigated in the present report. It is of interest that if one uses a 2 to 1 ratio between discharge rates elicited by opposing movements in the same axis as a definition of directional selectivity, Dixon and Stein (*15*) have observed that 56 percent of the cells in the normal hamster's superior colliculus are directionally selective.
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Phase Sensitivity in Electroreception

Abstract. *The gymnotoid electric fish* Hypopomus artedi *discriminates between electric stimulus pulses with identical spectral amplitudes but different spectral phase functions. Behavioral results can be explained on the assumption that electroreception is based on a linear filter, approximately matched to the species' electric organ discharge. The impulse response of the appropriate matched filter, in fact, resembles the known impulse response of the electroreceptors involved.*

Electric organ discharges (EOD's) in gymnotoid electric fish show high interspecific but negligible intraspecific variation. They are reliable cues for species identification (*1-3*). Electroreceptors are most sensitive to stimuli with peak power frequencies near that of the particular species' EOD (*2, 4, 5*) and very similar "tuning" curves have been obtained in behavioral experiments (*6*). Electric fish are thus most sensitive to EOD's of their own species and the variability of EOD's across sympatric species should therefore enhance reproductive isolation (*7*).

In previous behavioral and electrophysiological experiments thresholds and intensities of responses were measured as functions of the peak power frequency of the stimulus applied. Discrimination of spectral phase functions alone was not tested, except in studies which demonstrated that receptors responded differently to positive and negative square pulses (*8*), two stimuli with identical amplitude spectra (Fourier transform magnitudes) but spectral phase functions which differ by 180°. The behavioral studies of the gymnotoid *Hypopomus artedi* reported here show that this species can discriminate EOD-like stimulus pulses of identical amplitude spectra but with spectral phase functions which differ by a frequency-independent shift of as little as 45°. Such pulses are indistinguishable in the realm of human hearing.

Spectral phase sensitivity indicates that the specific shape of a temporal EOD wave form is important to the animal. An unbounded number of different wave forms have the same spectral amplitude, but the specification of both amplitude and phase in the frequency domain results in a uniquely defined time signal. Phase sensitivity should be of particular significance for discrimination between ohmic and capacitive features in the electric environment of the animal (*4*).

Hypopomus artedi fires its electric organ to produce diphasic pulses approximately 2 msec in duration [Fig. 2a, upper left; see also (*9*)], as measured by two electrodes with the positive electrode near its head and the negative electrode near the tip of its tail. Maximal spectral power of a single EOD is found near 550 Hz. The EOD's occur at a regular repetition rate near 10 Hz when the animal is resting. Novel stimuli cause sudden accelerations in the EOD rate, which may rise as high as 50 Hz. This novelty response was exploited to measure detection thresholds for various EOD-like stimulus pulses.

Single specimens, ranging in length from 15 to 22 cm, were placed in longitudinal cages 25 cm long, 3 cm wide, and 10 cm deep built out of plastic window screen. The cages were provided with loose peat moss strands for the animals to hide in. Each cage was placed in the center of an aquarium 60 cm long, 52 cm wide, and 18 cm deep, with the bottom of the cage approximately at middle water level. Water resistivity was 10 kilohm-cm and temperature was maintained between 24° and 27°C. Electric stimuli were provided through a pair of carbon rods, mounted at either end of the aquarium, which provided a near-homogeneous electric field in the area of the animal's cage. The intensity of stimulus pulses was measured in millivolts per centimeter, peak to peak, along the maximal field gradient in the center of the aquarium, in the absence of animal and cage. Stimulus pulses were generated by a PDP 11/40 computer, with a digital-to-analog converter operating at a sampling rate of 50 kHz. To obtain stimuli of sufficient power the output of this converter was passed through a Grass P15 preamplifier operating at × 10 amplification and at its widest frequency band, 0.1 Hz to 50 kHz. The output of this amplifier was connected to the stimulus electrodes; its d-c deviation from zero was maintained within 1.5 percent of the peak-to-peak stimulus amplitude.

The animal's EOD's were recorded by a pair of differential electrodes near its tail region. These electrodes were placed on an isopotential of the stimulus field to exclusively record the animal's EOD's. The instantaneous EOD rate was measured as the inverse of the intervals between EOD's by on-line computation. After 60 EOD's, each of the subsequent 40 EOD's was echoed, at a delay of 30 msec, by a stimulus pulse. An additional 60 poststimulatory EOD's were recorded thereafter. The 30-msec delay ensured that EOD's and stimuli would never overlap in time. The time course of instantaneous EOD rate recorded during this experiment was displayed by the computer for visual inspection. In an undisturbed and quietly resting animal the prestimulatory EOD rate showed a coefficient of variation of less than 1 percent. In response to suprathreshold stimulation a slight rise and increased variability in EOD rate was observed. This response started after the first three or four EOD's had been echoed. Its strength was measured by the root-mean-square (rms) value of the difference between the EOD rate during stimulation and its mean prestimulatory level.

Experiments were performed at intervals of at least 1 minute to minimize habituation to the stimulus. Records with large irregularities in EOD rate, which were commonly caused by sudden disturbances but also appeared to occur spontaneously, were discarded. The rms values of at least ten successive experiments were averaged for a particular type of stimulus pulse to yield a mean rms value, *S*, and different types of stimulus pulses were tested repeatedly, in intermingled order, by such series of experiments. With N series of experiments ($8 \leq N \leq 12$) conducted for a particular stimulus the mean, $\bar{S}$, and standard deviation (S.D.) of the averaged rms values, S, were calculated. The $\bar{S}$ values could be normalized with regard to $\bar{S}_0$, the baseline rms value obtained in the absence of stimulation.

In the first set of experiments single-period sinusoids of period duration $1/f_0$ (*10*) were presented as a stimulus at various intensities and, by interpolation, the particular intensity, I, was determined at which the normalized response $\bar{S}/\bar{S}_0$ reached a value of 2. A single-period sinusoid of period length $1/f_0$ has a peak power frequency at approximately $0.84 \times f_0$. The data in Fig. 1a demonstrate the lowest detection thresholds near $f_0 = 700$ Hz, which represents a peak power frequency of $f = 0.84 \times 700 = 588$ Hz. This value is slightly above the peak power frequency of the EOD of this species. Very similar tuning curves were obtained in electrophysiological studies of two types of tuberous electroreceptors, pulse marker units and narrow-band burst duration coders, and both were found to be most sensitive to frequencies slightly above the peak power frequency of the species' EOD (*2, 5*). Since pulse marker units have firing thresholds on the order of 10 mV/cm at their most sensitive frequency and in a transversely oriented stimulus field (*5*), the behavioral response in Fig. 1 appears to be driven by the more sensitive narrow-band units.

To test the significance of the spectral phase of the stimulus, the EOD of *H. artedi* was transformed by shifting the phases of all its positive frequency components by $n \times 45°$ and the phases of all its negative frequency components simultaneously by $-n \times 45°$, with $n = 0, 1, 2, \ldots 7$. The resulting stimulus pulses, which all have identical amplitude spectra, are shown in Fig. 2a. A shift of 0° represents the natural EOD, a shift of 180° its negative version. Stimuli were presented longitudinally to the animal, which faced the negative electrode. Presentation of the original EOD thus yielded a pattern of current flow similar to that associated with the animal's own electric organ activity; that is, during the first phase of the stimulus, current flowed out of the animal's head. Figure 1b presents data for two animals. A near-threshold stimulus intensity, 2 mV/cm peak-to-peak in the case of the non-transformed EOD stimulus, was chosen to avoid saturation of response amplitude. Even though all stimulus pulses had the same spectral power, the specimens responded differentially depending on stimulus pulse shape (phase).

The behavioral data in Fig. 1, a and b, can be interpreted on the assumption that tuberous electroreceptors operate, within near-threshold range, in a manner that is mathematically equivalent to the operation of a matched filter followed by a threshold detector. A filter matched to a particular signal, $v(t)$, processes any incoming signal, $u(t)$, by cross-correlating v and u. The function $v(t)$ is the time-reversed version of the filter's impulse response, $v(-t)$. If a threshold detector is applied to the time function, $r(\tau)$, that appears at the filter output, then the response strength, R, should be proportional to the positive peak, $r_{\max} = \max r(\tau)$ $(-\infty < \tau < \infty)$, of the filter output—that is, the maximum value of the cross-correlation function (*11*)

$$r(\tau) = \int_{-\infty}^{\infty} v(t)\, u(t + \tau) dt$$

The data points in Fig. 1a represent the threshold stimulus amplitudes, I, that are required for single-period sinusoids with different periods, $1/f_0$, to be detected by the fish. With $u(t)$ an amplitude-

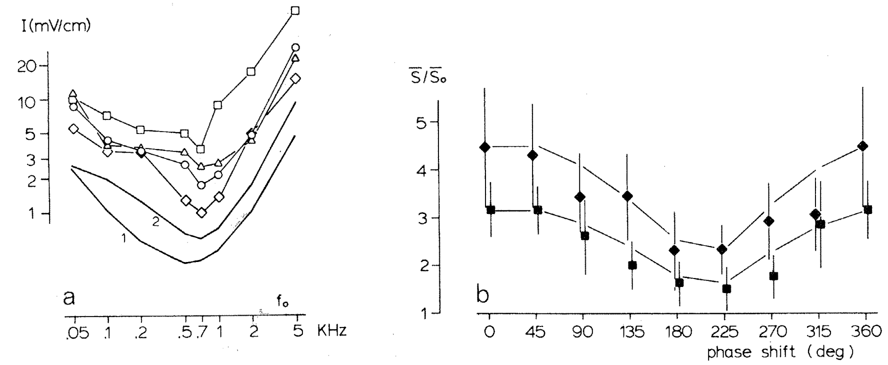

Fig. 1. (a) Behavioral tuning curves of four specimens of *H. artedi*. The ordinate indicates the critical stimulus intensity, I, required to elicit minimal responses of strength $\bar{S}/\bar{S}_0 = 2$ (see text). Stimulating electrodes were oriented transversely to the animal. Stimulus intensities approximately four times smaller are required if stimuli are applied longitudinally. The peak power of the EOD was between 450 and 550 Hz in all specimens. Lowest response thresholds were obtained with single-period sinusoids of period duration $1/f_0$ where $f_0 = 700$ Hz, which has its peak power at 588 Hz. Curves 1 and 2 indicate the shape of the tuning curves predicted on the assumption that receptors are filters matched to pulses 1 and 2, respectively, in Fig. 2b. These curves represent the reciprocals of maximal cross-correlations, $r_{\max}^{-1}$, between amplitude-normalized, single-period sinusoids of period duration $1/f_0$ and pulses 1 and 2, respectively. Their absolute values are arbitrary. (b) Mean strength of the response to the EOD and its phase-shifted versions (abscissa) presented in Fig. 2a for two individuals. For each type of stimulus at least ten S values were averaged for individual ◆ and at least seven for individual ■. Highest and lowest $\bar{S}/\bar{S}_0$ values are significantly different ($P < .001$; Student's t-test for either animal. The stimulus was applied longitudinally, with the negative electrode in front of the animal's head. All stimuli had identical power, and the peak-to-peak amplitude was 2 mV/cm for the unshifted stimulus. The continuous curves give values predicted on the assumption of a filter matched to pulse 2 in Fig. 2b. These curves represent maximal cross-correlations between stimulus pulses of Fig. 2a and pulse 2 of Fig. 2b. They were scaled differently for each animal to approximate the data points. Vertical bars give standard deviations.

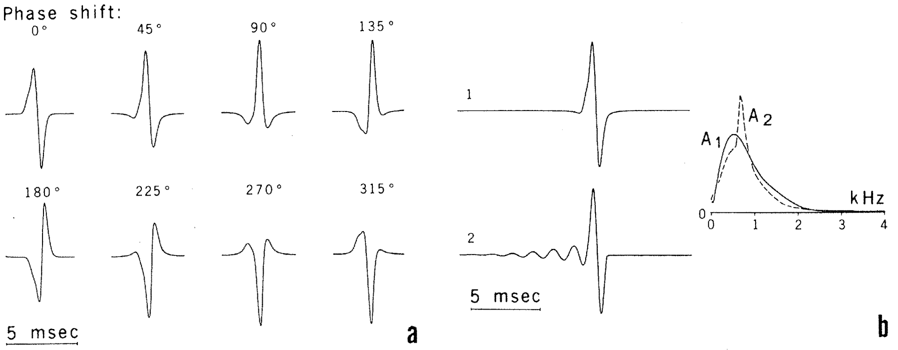

Fig. 2. (a) The EOD of *Hypopomus artedi* (top left record; positive is up; the positive recording electrode was in front of the head and the negative electrode behind the tip of the tail) and its transformations obtained by adding multiples of 45° to the spectral phases of all positive frequencies and equal multiples of −45° to the spectral phases of all negative frequencies. All eight pulses have identical power spectra. (b) Pulse 1 is the EOD pulse with a 22.5° phase shift. Pulse 2 was obtained by modifying the amplitude spectrum of pulse 1 and by eliminating oscillations in the right half. Each pulse can be considered as the time-reversed impulse response of a matched filter. The energy-normalized linear amplitude spectra of pulse 1 (A_1) and pulse 2 (A_2) are shown on the right.

normalized sinusoid, the stimulus would be $I\,u(t)$, and $I \max r(\tau)$, with $r(\tau)$ given by the integral above, has to meet a constant threshold response, R_0 for the stimulus function, $u(t)$, to be detectable. As a consequence, the gain, I, that is required to exceed the threshold in Fig. 1a should be proportional to $[\max r(\tau)]^{-1}$. The data points in Fig. 1b, on the other hand, represent response amplitudes, R, for different stimuli, $u(t)$, with identical power, as shown in Fig. 2a, and R should consequently be proportional to $\max r(\tau)$.

If the form of the filter impulse response, $v(-t)$, is given, one thus can predict the responses, shown in Fig. 1, to different stimulus pulses, $u(t)$. The accuracy of such a prediction depends on the validity of our assumptions and on the accuracy with which $v(-t)$ approximates the filter that presumably exists in the fish.

One may ask whether a single electroreceptor is really capable of completely simulating the effect of a matched filter, or whether it is merely one component of a filtering operation that is performed at various stages of the fish's afferent system. Additional data (*12, 13*) seem to indicate that all of the filter's operations are actually carried out by a single, peripheral electroreceptor.

The data in Fig. 1b can readily be approximated under the assumption that the filter is matched to the EOD, phase-shifted by 22.5°; that is, with $v(t)$ being pulse 1 in Fig. 2b. However, the tuning curve predicted by this model for Fig. 1a (curve 1) is less satisfactory. It lacks the minimum at $f_0 = 700$ Hz which characterizes all behavioral data, and climbs too steeply in the low-frequency range. To improve this data approximation, the amplitude of the filter transfer function was modified, mainly by raising power between 50 and 100 Hz and between 700 and 800 Hz until a theoretical tuning curve was obtained which most closely resembled the behavioral data in Fig. 1a. This adjustment in the frequency domain caused the resulting signal, $v(t)$, in the time domain to acquire small oscillations before and after the main part of the pulse. Since $v(t)$ is the time-reversed version of the filter's impulse response and since the latter is assumed to start with a sudden large amplitude rather than with a gradual buildup, the small oscillations in the right half of the resulting pulse (pulse 2 in Fig. 2b) were eliminated. A time-reversed version of pulse 2 in Fig. 2b strongly resembles the "ringing" impulse response reported in various gymnotoid electroreceptors (*12, 13*). The elimination of the small oscillations on the right side of the pulse still allowed for a tuning curve that closely resembled the behavioral data (curve 2 in Fig. 1a). Relative response strengths that are predicted from a matched-filter assumption, where $v(t)$ is curve 2 in Fig. 2b, are indicated by the piecewise linear curves in Fig. 1b.

Filter function 2 in Fig. 2b may not provide the best approximation of the behavioral data in Fig. 1, but it gives better predictions than any phase-shifted version of the animal's EOD such as pulse 1 in Fig. 2b. The fact that the electroreceptive system of *H. artedi* is not matched to the species' own EOD but rather to a distorted version of this signal could be interpreted in the following manner.

The behavioral response exploited in these experiments is obviously tuned to EOD's of a distant conspecific and, as mentioned previously, most likely driven by narrow-band units (*9*). If narrow-band units evolved mainly for the purpose of detecting a conspecific's EOD's to enhance social communication among species members (*7*), they should not only be tuned to the species' EOD but should also be least sensitive to EOD's of different sympatric species. *Hypopomus artedi* lives sympatrically with four additional species of the same genus in muddy habitats of the Rio Negro (*3*). The EOD's of all the species differ in their peak power frequency. The most abundant species, next to *H. artedi*, is still taxonomically undescribed. It is closest to *H. artedi* with regard to its peak power frequency, which averages 410 Hz (S.D. = 90 Hz) while *H. artedi*'s peak power frequency averages 560 Hz (S.D. = 60 Hz) (*14*). If filter functions 1 and 2 in Fig. 2b are cross-correlated with energy-normalized EOD's of these two species, filter function 1 is almost equally sensitive to either EOD, whereas filter function 2 responds with a 1.3 times higher maximum value of the correlation function to the EOD of *H. artedi*.

By tuning a particular type of electroreceptor more narrowly, *H. artedi* thus minimizes species cross talk. However, one may wonder why *H. artedi* did not modify its EOD spectrum in a parallel manner. The slight mismatch between filter and species-specific signal may after all reflect evolutionary constraints. Physiological conditions of signal production and perception may not have allowed a better match between signal and filter functions. On the other hand, if the EOD of *H. artedi* were modified, might its neighbor not usurp the frequencies that were left unoccupied, thereby causing an even worse environment for *Hypopomus*' electrical communication? In this case, *H. artedi* would be defending its spectral "territory" with a signal that is partially designed to jam or inconvenience intruders.

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9. The EOD recording in Fig. 2a (top left curve) is obtained by placing the positive electrode in front of the animal's head and the negative electrode beyond the tip of its tail. This particular signal characterizes the peripheral current of the animal's EOD field, and a very similar signal should be perceived by the fish from a distant neighbor. The animal perceives a very different signal when it fires its own organ. The current pulse which penetrates the surface of the anterior body can be monitored by a narrowly spaced pair of differential electrodes, perpendicularly oriented and near the skin. Pulses recorded in this manner have large d-c components and dominant power around 200 Hz. Particular tuberous electroreceptors, "broad-band" and "low-frequency" burst duration coders (*2, 5*), are most sensitive in this low-frequency range and may be most important in the evaluation of the animal's own feedback. Two further types of tuberous electroreceptors, "narrow-band" burst duration coders and "pulse marker" units, have tuning curves very similar to those in Fig. 1a and are most sensitive at frequencies slightly above the dominant frequency of the distantly recorded EOD (*2, 5*). The threshold data in Fig. 1a, as mentioned in the text, suggest that only narrow-band units are involved in the behavioral response of Fig. 1.
10. A single-period sinusoid of period duration $1/f_0$ and amplitude A is defined as $A \sin(2\pi f_0 t)$ for $0 \leq t \leq 1/f_0$ and is zero otherwise.
11. This model is slightly different from the conventional use of matched filters in radar systems. For radar applications, the filter is followed by a squarer and integrator (envelope detection), and the resulting envelope is passed through a threshold. In our electroreceptor model, the filter response is passed directly to a threshold device. The model also differs from the use of matched filters in synchronous communication systems, where signal arrival time is known beforehand. When arrival time is known, the filter output can be sampled at a prespecified time. This synchronous processing may be applicable to electroreception of an EOD that is generated by the animal itself. For unspecified arrival time, however, an observer must scan the matched filter response in order to find the maximum output, and a decision about the presence or absence of a signal is based on this maximum response. These scanning and comparison operations are accomplished with a threshold that "fires" when the input signal exceeds a specified level.
12. T. Viancour, abstract 335, Neurosciences Meeting, Toronto, Canada, 1976.
13. T. Viancour (personal communication) inferred ringing impulse responses in electroreceptors of

Rhamphichthys which fires its electric organ in discrete pulses much as *Hypopomus* does. A burst duration coder in *Hypopomus*, with maximal sensitivity at the spectral frequency f, fires a series of spikes in response to a stimulus pulse, with an initial spike frequency near f [T. H. Bullock, *J. Gen. Physiol.* **55**, 563 (1970); J. Bastian (*5*)]. This supports the assumption that the receptor rings at this frequency and that one spike is triggered on each suprathreshold cycle (C. D. Hopkins, personal communcation).

14. This measurement is based on 40 specimens of each species from Rio Negro habitats (*3*).
15. Supported by grants from the National Science Foundation (BMS 76-20761) and the National Institute of Mental Health (PHSMH 2614901) to W.H. We are most grateful to T. H. Bullock, J. Thorson, C. Hopkins, C. Baker, J. Bastian, T. Viancour, and two anonymous referees for most helpful criticisms.

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Infrared Video Viewing

The use of video to render visible the ordinarily invisible ultraviolet patterns found in nature has been described (*1*). We now describe a similar system for video viewing in the near infrared (700 to 1000 nm) which permits both the visualization of infrared patterns (*2*) and the study of nocturnal behavior. In this system (*3*) a commercially available video camera is fitted with an optional silicon diode imaging tube originally developed for low light level surveillance. The spectral sensitivity of the silicon diode tube spans the visible range (400 to 700 nm) and extends beyond 1000 nm, thereby including the near-infrared region. These spectral properties can be used to advantage in the investigation of various biological problems.

The nocturnal behavior of animals is difficult to observe and record. The lighting necessary for conventional photography, cinematography, videotaping, or direct observation may inhibit or alter the animal's behavior. Use of the silicon diode camera, however, permits illumination in the near-infrared region where most animals appear to be blind (*4-7*). We have used this technique to study the nocturnal courtship of an arctiid moth, *Utetheisa ornatrix*, and nocturnal predatory behavior of the Florida mouse, *Peromyscus floridanus* (Fig. 1). The courtship of the moth is disrupted by most artificial light sources; however, normal courtship could be observed and recorded under infrared illumination. In the mouse study, complete darkness was required since the purpose of the study was to investigate predatory behavior when visual information is limited. Again, the fact that the camera is sensitive in a region where the subject is not sensitive permitted videotaping of this behavior. Our experience, therefore, suggests that infrared video viewing will prove generally useful in the study of nocturnal behavior.

Other methods available for viewing in darkness include infrared photography and cinematography, infrared imaging devices (for example, "sniper scopes"), and light amplifying devices ("starlight scopes"). Compared with these, infrared video has the familiar advantages of conventional video which include simultaneous monitoring and storage and instant playback. Also, although we have not done so, the video system could easily be made portable in the field, as are many infrared imaging and light amplifying devices. The quality of the video image is good, although a sharper image can be obtained through the more laborious techniques of infrared photography and cinematography. The starlight scope functions at even lower light intensities than the video system described. At present, though, this instrument is substantially more expensive than infrared video and is not as generally available. In many situations, therefore, the silicon diode video system seems to offer significant advantages. Furthermore, the system is not restricted to use in the infrared or at low light levels; it can be used without modification in visible light and at normal illumination levels.

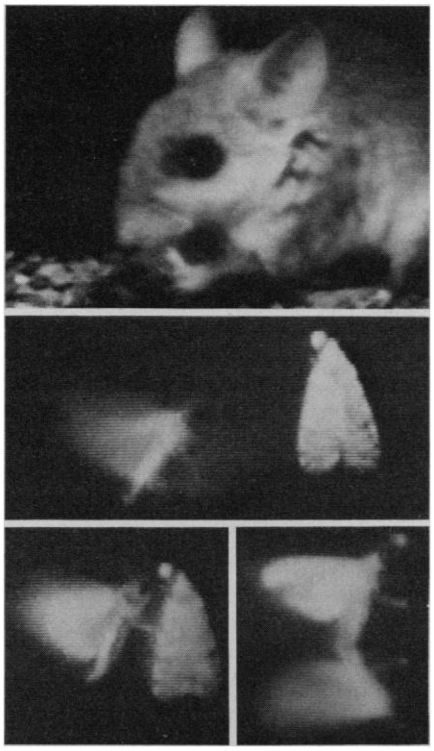

Fig. 1. (Top) Mouse feeding in total darkness. (Bottom) Sequential views of moth courtship showing a male approaching a stationary female, orienting to her, and copulating. All photographs are of infrared images as they appear on a television screen. To freeze the image for photography the video recorder was operated in the stop-action mode. This results in a marked decrease in image resolution. The fully interlaced video picture obtained during normal playback yields a significantly sharper image.

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3. We use a General Electric video camera (model TE44BS) with a silicon diode imaging tube (No. 7164425P94). We record on either of two Sony videocorders (model AV5000A or the more portable model AV3400). The image can be displayed on any closed circuit television monitor. Infrared images are obtained by operating the system in total darkness with illumination provided by two 40-watt incandescent lamps that shine through infrared filters. The transmittance of the filters is less than 1 percent below 900 nm and less than 0.03 percent below 700 nm.
4. Since evidence on visual sensitivity in the near infrared is extremely scarce, the possibility exists that some animals can form visual images under infrared illumination. To date, however, no infrared-sensitive visual pigment has been discovered (*5*). Furthermore, tests of the spectral sensitivity of animals by behavioral methods suggest that the infrared limit of vision does not surpass that of humans (*6*), although, unfortunately, actual tests at longer wavelengths have apparently not often been done. Of course the definition of the limit of vision is arbitrary since sensitivity falls off gradually. Humans can detect radiation at 1000 nm, for instance, but at this point sensitivity is reduced to approximately 10^{-12} of the best sensitivity (*7*).
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22 November 1977