island age, gives a plot of the corrected species diversity, S^*, as a function of the time since isolation. This plot is given in Fig. 1.

This result is equivalent to a plot of species diversity as a function of time (or, a relaxation curve) for a hypothetical island with mean area and latitude. A linear regression of log transformed values of both variables produces a fitted curve described by the exponential function

$$S^* = 10^6 T^{-1.13}$$

with a correlation coefficient of $-.82$ ($P < .01$). Thus S^* represents a standardized level of species diversity to which each fauna has relaxed up to the present time. The relaxation process has both an immigration and extinction component. Since immigration is not detectable, however, the relaxation curve here is approximately equivalent to an extinction curve. These results are consistent with the hypothesis that these are nonequilibrium supersaturated faunas which are relaxing to states with fewer species.

Recently, Simberloff (*3*) questioned the validity of the equilibrium theory of island biogeography, citing a lack of rigorous proof of species turnover, or evidence that a fauna is approximately balanced, within an ecological time scale (*17*). The demonstration that nonequilibrium biotas behave dynamically in predicted ways is perhaps better evidence for the equilibrium theory than is the existence of biotas in apparent equilibrium. Thus, the equilibrium condition could be considered just one possible state predicted by the theory.

BRUCE A. WILCOX
Department of Biology, University of California, San Diego, La Jolla 92093

References and Notes

1. R. H. MacArthur and E. O. Wilson, *The Theory of Island Biogeography* (Princeton Univ. Press, Princeton, N.J., 1967).
2. For example, applications of the theory have been attempted for diatom communities [R. Patrick, *Proc. Natl. Acad. Sci. U.S.A.* **58**, 1335 (1967)], plant communities [M. P. Johnson and P. R. Raven, *Science* **179**, 893 (1973)], bird communities (*4, 5, 9*), lizard communities (*6, 7*), and conservation [(*8*); J. M. Diamond, *Biol. Conserv.* **7**, 129 (1975)].
3. D. Simberloff, *Science* **194**, 572 (1976).
4. J. M. Diamond, *Proc. Natl. Acad. Sci. U.S.A.* **67**, 1715 (1972).
5. J. Terborgh, *BioScience* **24**, 715 (1974).
6. M. Soulé and A. J. Sloan, *Trans. San Diego Soc. Nat. Hist.* **14**, 137 (1966).
7. T. J. Case, *Ecology* **56**, 3 (1975).
8. D. S. Simberloff and L. G. Abele, *Science* **191**, 285 (1976).
9. I. Abbott and P. R. Grant, *Am. Nat.* **110**, 507 (1976).
10. Constituents of the species pool for the region adjacent to each island were determined with range maps from R. C. Stebbins [*A Field Guide to the Western Reptiles and Amphibians* (Houghton Mifflin, Boston, 1966)]. The pool size was taken as 15 for all but five islands. The exceptions were Tiburon, 13; Cedros and Natividad, 12; San Francisco, 11; and Mejia, 8.
11. J. M. Savage, in *Proceedings of the Symposium on the Biology of the California Islands*, R. N. Philbrick, Ed. (Santa Barbara Botanic Garden, Santa Barbara, 1967), p. 219.
12. The general importance of A, D, and E as biogeographic variables has been established; see (*1*) and T. H. Hamilton, I. Rubinoff, R. H. Barth, Jr., G. L. Bush, *Science* **142**, 1575 (1963). However, L and T are explained as follows. *Latitude*: the islands in this study occur over a latitudinal gradient of more than 5 degrees, with the northernmost extending into a Mediterranean climatic zone and the southernmost into an arid-subtropical zone [J. R. Hastings and R. M. Turner, "Meteorology and climatology of arid regions," *Univ. Ariz. Inst. Atmos. Phys. Tech. Rep. No. 18* (1969)]. Associated with this climatic difference is an increasing structural and taxonomic diversity of the vegetation southward [F. Schreve and I. L. Wiggins, *Vegetation and Flora of the Sonoran Desert* (Stanford Univ. Press, Stanford, Calif., 1964), vols. 1 and 2; J. R. Hastings and R. M. Turner, "Meteorology and climatology of arid regions," *Univ. Ariz. Inst. Atmos. Phys. Tech. Rep. No. 21* (1972)]. The moderating effect of the subtropical climate and the increased structural diversity of the habitats should improve the chances of species coexistence [E. R. Pianka, *Ecology* **48**, 333 (1967)] and thus increase successful colonizations and reduce extinctions. *Age*: an examination of the submarine topography surrounding these islands (Defense Mapping Agency Hydrographic Charts, Nos. 21005, 21008, 21011, and 21014) reveals that each island is now separated from the mainland by a minimum ocean depth that may range from 11 to 93 meters. Since this region has been relatively tectonically stable during postglacial times (G. Gastil, personal communication) it should be possible to estimate the dates of isolation of each island from the mainland on the basis of the rate of post-Wisconsin eustatic sea level rise with time. The general features of the eustatic sea level rise with time have been established by an accumulation of corroborative evidence [F. P. Shepard and J. R. Curray, *Prog. Oceanogr.* **4**, 283 (1967); J. D. Milliman and K. O. Emery, *Science* **162**, 1121 (1968); A. L. Bloom, "Glacial isostatic and eustatic controls of sea level change since the last glaciation," in *The Late Cenozoic Glacial Ages*, K. Turekian, Ed. (Yale Univ. Press, New Haven, Conn., 1971)], p. 355. This evidence suggests an approximate scheme of sea level rise with time as summarized in a plot by Milliman and Emery (cited above). From their curve, I have estimated the dates of isolation for each island by extrapolation from the ocean depth between each island and the mainland.
13. The values 100 and 10,000 were also used for the mainland area. However, similar results were obtained in the correlation analysis regardless of the value used.
14. B. A. Wilcox, in preparation.
15. The residuals were calculated from the regression equation
$$S = 440 + 23(\log A) - 294(\log L)$$
16. This step results in the elimination of negative residuals and allows for log transformation of S^* values.
17. Subsequently, J. M. Diamond and R. M. May [*Science* **197**, 266 (1977)] have shown that existing evidence may be stronger than was previously apparent.
18. I thank M. Soulé for continued help throughout this study and M. Rosenzweig and J. Senner for helpful suggestions. This work was supported by NIH grant 6M 07242, NSF grant DEB 76-18604, and the Theodore Roosevelt Memorial Fund.

22 August 1977; revised 31 October 1977

Directional Selectivity in Hamster Superior Colliculus Is Modified by Strobe-Rearing But Not by Dark-Rearing

Abstract. *Visual response properties of superior collicular neurons of normal hamsters were compared with those of animals reared from birth to adulthood in either total darkness or with stroboscopic illumination. Directional selectivity was markedly reduced only in the strobe-reared animals, thus demonstrating visual plasticity in a system that develops apparently normally without visual experience.*

Since the early 1960's many studies have been concerned with the role of early experience in the functional organization of the brain's visual centers (*1, 2*). Two types of manipulations have been commonly employed: (i) visual deprivation, attained by dark-rearing or eyelid suturing; and (ii) visual restriction, in which the animal's early experience is limited along one or more stimulus dimensions. Most of these studies have dealt with the visual system of the cat, and in this species dramatic effects of visual deprivation, as well as restriction, have been demonstrated in the cortex and, more recently, in the superior colliculus (*3–5*). However, there appear to be important species differences with regard to the degree of plasticity exhibited by the mammalian visual system. Thus, in rabbit, visual restriction during development failed to modify the functional organization of single neurons in visual cortex (*6*). Furthermore, in comparison to the cat, visual deprivation in rabbit results in relatively subtle effects upon the response characteristics of either cortical or superior collicular neurons (*2, 7*).

We now report a demonstration of plasticity in response to environmental restriction in a visual system that develops relatively normally without visual experience. These results were obtained in the golden hamster (*Mesocricetus auratus*), where we have found that dark-rearing produces only subtle changes in the receptive-field properties of superior collicular neurons, whereas rearing in a stroboscopic environment results in dramatic modifications in the functional organization of this midbrain structure. The most clear-cut effect of stroboscopic rearing was on directional selectivity, and this finding is the main focus of this report (*8*).

We used three groups of animals: group 1 included normal hamsters, reared on a 12-hour light/dark cycle ($N = 33$); group 2 included visually deprived animals, raised from birth to adulthood in total darkness ($N = 13$); and group 3 included visually restricted hamsters that were raised from birth to adulthood in an environment illuminated for 12 hours each day with very brief (4 μsec) flashes at the rate of two per second ($N = 14$). The last condition deprives animals of experience with moving stimuli while allowing pattern vision. The strobe rate we employed modifies the receptive-field characteristics of cells in the cat's superior colliculus (*5*). It should be noted that the dark- and strobe-reared animals were kept in their respective environments until the day of recording which occurred when the animals reached adulthood, at least 5 months of age. Animal maintenance was carried out in total darkness or with strobe illumination. Repeated checks were made to ensure that the appropriate rearing conditions were maintained.

Extracellular recordings from the superior colliculus of paralyzed, lightly anesthetized (sodium pentobarbital), and artificially respirated hamsters were obtained with high-impedance (20 to 30 megohms measured at 1 kHz) tungsten microelectrodes. Retinoscopy was not employed in these experiments because this procedure results in systematic errors of hypermetropia with an eye as small as that of the hamster (*9*). Further, it has been noted by others that such a small eye should have a very large depth of focus and this point has been demonstrated empirically in the hamster (*10*). After isolating the electrical activity of a single cell we plotted its receptive field on a tangent screen using light and dark hand-held stimuli 2.5 log units above to 1 log unit below a 1.4 cd/m² background. Cells were tested for speed preferences and directional selectivity, as well as for

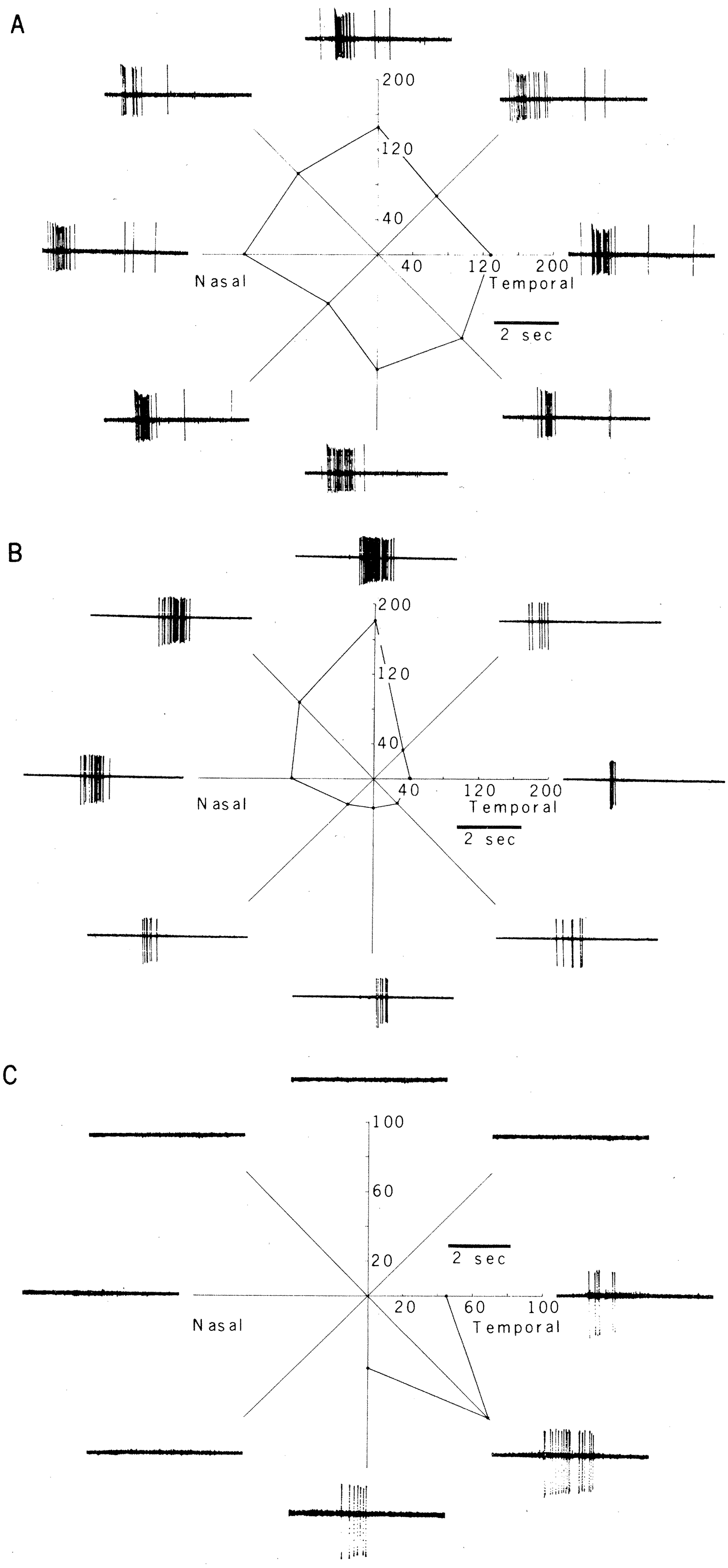

Fig. 1. (A) Polar diagram and representative oscilloscope traces depicting the responses of a cell that showed no directional selectivity recorded from the superficial collicular laminae of a strobe-reared hamster. Each point on the diagram represents the summed responses obtained in five stimulus presentations. The stimulus was a 6° light spot swept across the receptive field at a velocity of 15° per second. The size of the receptive field was 8° by 11°, and this cell had no spontaneous activity. (B) The responses of a cell that exhibited a statistical preference for stimuli moving in an upward and nasal direction. This cell was recorded from the superficial collicular layers of a normally reared hamster. It had no spontaneous activity and responded reliably to stimulus movement in each of the directions tested. The stimulus was a 4° light spot moving at 10° per second. The receptive field was 7° by 9.5°. (C) The responses of a cell that was directionally selective by the "null" criterion. This cell was recorded from the superficial collicular laminae of a normally reared hamster. Its receptive field measured 12° by 10.5°, and the cell had no spontaneous activity. The stimulus was a 2.5° light spot which was moved across the receptive field at 5° per second.

responses to stationary flashed stimuli of various sizes (*11, 12*). For testing directional selectivity a specially constructed visual stimulator moved spots of light at specified speeds across the receptive field in each of four axes: vertical, horizontal, and the two oblique axes bisecting these quadrants. Typically, for a given cell, only that stimulus speed which was close to the preferred velocity was employed. Each of the eight directions of stimulus movement was tested at least five times, with an interval between trials of about 10 seconds.

The number of action potentials (spike count) evoked by each stimulus presentation was read directly off the face of a storage oscilloscope, and in some cases responses were recorded on tape for offline analysis. For each cell, directional selectivity was assessed in two different ways: statistically and with the "null" criterion. With the statistical criterion, t-tests were computed for responses to opposing directions of movement, and any cell that showed significant ($P < .05$) response asymmetry was considered to be directionally selective. With the "null" criterion a cell was judged as directionally selective if it responded to movement in one direction and showed no reliable responses or suppression of spontaneous activity with movement in the opposing direction (*13*). The loci of representative cells were marked by making electrolytic lesions (35 μA for 2 seconds). Animals were perfused through the heart with saline followed by buffered formalin, and the brains were removed and cut in paraffin at 10 μm for histological reconstruction of electrode tracts.

Figure 1 shows the responses of three cells. In Fig. 1A the cell responded to movement in all directions with an approximately equal number of discharges. In contrast, B and C of Fig. 1 illustrate the responses of cells that were directionally selective with the statistical (Fig. 1B) and the "null" (Fig. 1C) criteria. In normal hamsters, 173 cells were tested for directional selectivity and of these, 99 (57.2 percent) were found to be directionally selective according to the statistical criterion, whereas 46 cells (26.6 percent) exhibited selectivity as defined by the "null" criterion (*14, 15*). Of the 93 cells tested in dark-reared animals, 51 (54.8 percent) were judged as selective statistically, while 26 (27.9 percent) had a preferred and null direction. In strobe-reared animals 110 neurons were tested and 26 (23.6 percent) showed significant response asymmetry to opposing directions of movement, whereas only seven cells (6.4 percent) were directional with the "null" criterion (*14*). These findings are summarized in Fig. 2.

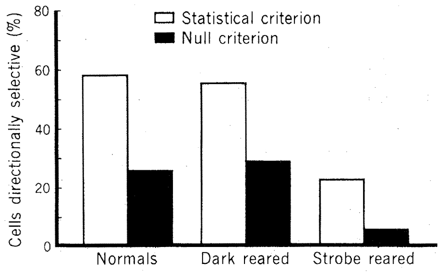

Fig. 2. The percentage of directionally selective cells as judged by the statistical and "null" criteria for the three groups of hamsters used in this study. The bar graph indicates a clear decrease in the percentage of directionally selective cells as judged by either criterion for the strobe-reared hamsters.

Dark-reared hamsters also could not be differentiated from normal animals on the basis of the distribution of the preferred directions of the directionally selective cells. Furthermore, speed preferences, receptive-field size, and organization were the same in both groups. There were however, differences in the onset latencies of neurons which responded to flashed stimuli in that these were longer in the visually deprived animals. In addition, a few cells in the dark-reared hamsters responded in a sustained fashion to flashed spots of light, whereas in normal animals all cells responded only phasically to light onset or offset, or both.

While the decrease in the incidence of directionally selective cells was the most dramatic effect of strobe-rearing, other differences were also observed. One of these was a reduction in the number of cells showing response suppression when stimuli larger than the activating region of the receptive field were employed. Further, cells in the superficial layers of the colliculus (those dorsal to the stratum griseum intermediale) often exhibited considerable response variability, an observation common for cells in the deeper layers of normal and dark-reared animals but rare for cells of the superficial layers.

These findings indicate that in the golden hamster visual experience plays a minimal role in the maintenance or induction of the functional organization of the superior colliculus but that an aberrant visual input during development, in this case strobe illumination, can induce major changes in this system.

The only other species in which the functional organization of the superior colliculus has been examined after binocular deprivation (lid-suturing) and strobe-rearing is the cat. Here, both manipulations have been reported to result in a considerable decrease in the incidence of directionally selective neurons, as well as in modifications of other receptive-field characteristics (*4, 5*). The present findings, when compared to those in the cat, further underscore the importance of species differences with regard to visual system plasticity. Further delineation of the factors involved in visual system plasticity could be facilitated by the examination of this problem in other mammals, as well as nonmammalian species (*16*).

LEO M. CHALUPA
ROBERT W. RHOADES
Department of Psychology, University of California, Davis 95616

References and Notes

1. H. B. Barlow, *Nature (London)* **258**, 199 (1975); J. Daniels and J. D. Pettigrew, in *Neural and Behavioral Specificity*, G. Gottlieb, Ed. (Academic Press, New York, 1976), vol. 3.
2. P. Grobstein and K. L. Chow, *Science* **190**, 352 (1975).
3. T. N. Wiesel and D. H. Hubel, *J. Neurophysiol.* **26**, 1003 (1963); *ibid.* **28**, 1029 (1965); *ibid.* , p. 1060; D. H. Hubel and T. N. Wiesel, *J. Physiol. (London)* **206**, 419 (1970); C. Blakemore and G. F. Cooper, *Nature (London)* **228**, 477 (1970); H. V. B. Hirsch and D. N. Spinelli, *Science* **168**, 869 (1970); M. Cynader, N. Berman, A. Hein, *Proc. Natl. Acad. Sci. U.S.A.* **70**, 1353 (1973); J. D. Pettigrew and R. D. Freeman, *Science* **182**, 599 (1973); _____, L. J. Garey, *Brain Res.* **66**, 160 (1974); N. W. Daw and H. J. Wyatt, *J. Physiol. (London)* **257**, 155 (1976); M. Cynader and G. Chernenko, *Science* **193**, 504 (1976); C. Blakemore and R. C. Van Sluyters, *J. Physiol. (London)* **248**, 663 (1975).
4. K.-P. Hoffmann and S. M. Sherman, *J. Neurophysiol.* **37**, 1276 (1974); *ibid.* **38**, 1049 (1975); P. Sterling and B. G. Wickelgren, *Brain Behav. Evol.* **3**, 210 (1970); J. M. Flandrin and M. Jeannerod, *Brain Res.* **120**, 362 (1977); _____, H. Kennedy, B. Amblard, *ibid.* **101**, 576 (1976).
5. J. M. Flandrin and M. Jeannerod, *Brain Res.* **89**, 348 (1975).
6. R. R. Mize and E. H. Murphy, *Science* **180**, 320 (1973).
7. R. C. Van Sluyters and D. L. Stewart, *Exp. Brain Res.* **19**, 196 (1974); K. L. Chow and P. D. Spear, *Exp. Neurol.* **42**, 429 (1974).
8. More detailed accounts of the effects of dark- and strobe-rearing are provided elsewhere: R. W. Rhoades and L. M. Chalupa, *J. Comp. Neurol.* **177**, 17 (1978); L. M. Chalupa and R. W. Rhoades, *J. Physiol. (London)*, in press.
9. M. Glickstein and M. Millodot, *Science* **168**, 605 (1970).
10. U. C. Dräger and D. H. Hubel, *J. Neurophysiol.* **38**, 690 (1975); Y.-C. Tiao and C. Blakemore, *J. Comp. Neurol.* **168**, 459 (1976). To assure ourselves that there were no differences in the ability to resolve visual stimuli, we tested one normal and one strobe-reared animal with grating stimuli to activate visual neurons and used a series of corrective lenses to change the focus of the gratings on the retina. In each animal, we noted that eight diopters of positive or negative refraction did not alter the responses of collicular neurons. The additional finding that mean receptive-field size for a given depth in the superior colliculus did not differ significantly among the three groups of hamsters also indicates that the retinal images were focused on the retina approximately equally in the normal, dark-reared, and strobe-reared hamsters.
11. Details of the functional organization of the normal hamster's superior colliculus have been provided by R. W. Rhoades and L. M. Chalupa, *Brain Res.* **118**, 334 (1976); *Exp. Neurol.* **57**, 57 (1977); L. M. Chalupa and R. W. Rhoades, *J. Physiol. (London)* **270**, 595 (1977); see also (*12*).
12. Y.-C. Tiao and C. Blakemore, *J. Comp. Neurol.* **168**, 483 (1976).
13. H. B. Barlow and W. R. Levick, *J. Physiol. (London)* **178**, 477 (1965). It should be noted that each cell which exhibited directional selectivity

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.
15. J. Dixon and B. E. Stein, *Soc. Neurosci. Abstr.* **3**, 588 (1977).
16. J. D. Pettigrew and M. Konishi, *Nature (London)* **264**, 753 (1976).
17. We thank A. L. Morrow, M. S. Dias, and M. Leary for their assistance. Supported in part by Chancellor's Patent Fund and 1 RO3 MH29548-01 from National Institute of Mental Health.

25 June 1977; revised 17 October 1977

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 stim-

0036-8075/78/0303-1001$00.50/0