

as its input. The input fed to the computer was picked up from a bipolar pair of electrodes on the scalp, one mounted over the inion and the other about 5 cm anterior. The output of the computer, after it averaged the activity which followed 50 saccadic movements, was fed to an X-Y plotter. The ongoing brain activity, the raw eye-movement record, and the computer trigger signal were constantly monitored on an ink writer.

Continuously illuminated fixation targets were the only stimuli presented to the three observers; maximum retinal illuminance of the targets was 2×10^6 trolands. The illuminance could be varied in steps of 1.0 log unit over a range of 4.0 log units with neutral filters. The dimmest stimulus used was estimated by psychophysical means to be between 1.0 and 2.0 log units above absolute threshold. For one observer (J.K.) a single circular fixation spot 20 minutes in diameter produced reliable responses. The electroencephalogram records of the other two observers (K.G. and V.G.) had considerable "alpha" activity which made it difficult to evaluate the responses in the averaged records with this target. With the last two subjects a larger, more complicated target elicited useful records. This target had an overall diameter of 5 degrees and an internal grid structure consisting of 53 circular spots 20 minutes in diameter.

The experimental procedure was as follows. After alignment of the optical systems, the observer fixated the target at its lowest illuminance. The computer was activated, and the average of 50 samples of electrical brain signals was written on the plotter. The stimulus was then set at the next higher illuminance level and the process was repeated. An experimental session consisted of one ascending and one descending series of illuminances covering the whole 4.0 log unit range available. Each observer served in ten sessions.

A typical set of averaged records is given in Fig. 1. Each record showed a response consisting of a negative wave with an implicit time (or peak latency) of the order of 100 msec, followed by a positive wave which reached its peak by 250 msec. The waveform was sharply defined at the higher illuminances and more rounded and slower at the lower illuminances.

Averaged potentials recorded from the scalp exhibit complex and ephemeral waveforms (5). Since the purpose of our study was to determine whether any stimulus-determined response followed saccades, quantitative analysis was limited to the prominent negative-positive complex found in all records. Two measures were taken: (i) the implicit time or peak latency to the lowest negative point, and (ii) the amplitude from the lowest negative point to the highest positive point within the first 250 msec following the saccade. These measures are presented in Fig. 2. The implicit time of all observers was a monotonic decreasing function of fixation-target illuminance. In the case of J.K., the amplitude was a monotonic increasing function of illuminance. The amplitude curves for the other two observers were not simple functions of illuminance.

Because the observer is unaware of saccadic eye movements or of changes in the stimulus occurring during fixation, it is hard to attribute the responses to startle or variation in attention. The results indicate that a true evoked response is produced by the retinal image displacement accompanying saccadic eye movement, lending support to the idea that saccadic eye movements help to maintain vision. The results suggest that the nervous-system discharge accompanying vision may not be solely

continuous, but instead may be characterized by more or less discontinuous bursts related in time to saccades. This contrasts with the observer's reports that the fixation target appeared steady, a result which may have implications for theories of perception.

KENNETH GAARDER*

Chestnut Lodge Research Institute,
Rockville, Maryland

JOHN KRAUSKOPF

VIRGIL GRAF

University of Maryland,
College Park

WALTER KROPFL

JOHN C. ARMINGTON

Walter Reed Army Institute
of Research, Washington, D.C.

References and Notes

1. L. A. Riggs, F. Ratliff, J. C. Cornsweet, T. N. Cornsweet, *J. Opt. Soc. Amer.* **43**, 495 (1953); R. W. Ditchburn and B. L. Ginsborg, *Nature* **170**, 36 (1952).
2. J. Krauskopf, *J. Opt. Soc. Amer.* **47**, 740 (1957).
3. L. A. Riggs, J. C. Armington, F. Ratliff, *ibid.* **44**, 315 (1959). For more detail, see J. Krauskopf, T. N. Cornsweet, L. A. Riggs, *ibid.* **50**, 572 (1960).
4. Mnemotron Computer of Average Transients.
5. W. J. Rietveld, *Acta Physiol. Pharmacol. Neerl.* **12**, 373 (1963).
6. Supported in part by PHS grant MH 06554 to the Chestnut Lodge Research Institute (K.G.) and contract DA-49-193-MD-2327 between the Office of the Surgeon General, U.S. Army, and the University of Maryland (J.K. and V.G.).

* Present address: Clinical Neuropharmacology Research Center, St. Elizabeths Hospital, Washington, D.C. 20032.

1 October 1964

Culturally Transmitted Patterns of Vocal Behavior in Sparrows

Abstract. *Male white-crowned sparrows have song "dialects," acquired in about the first 100 days of life by learning from older males. In the laboratory an alien white-crowned sparrow dialect can be taught. Once the song is established further acoustical experience does not change the pattern. White-crowned sparrows do not copy recorded songs of other sparrow species presented under similar conditions.*

The white-crowned sparrow, *Zonotrichia leucophrys*, is a small song bird with an extensive breeding distribution in all but the southern and eastern parts of North America (1). Ornithologists have long remarked upon the geographical variability of its song. Physical analysis of field recordings of the several vocalizations of the Pacific Coast subspecies *Z. l. nuttalli* reveals that while most of the seven or so sounds which make up the adult repertoire vary little from one popu-

lation to another, the song patterns of the male show striking variation (see 2).

Each adult male has a single basic song pattern which, with minor variations of omission or repetition, is repeated throughout the season. Within a population small differences separate the songs of individual males but they all share certain salient characteristics of the song. In each discrete population there is one predominant pattern which differs in certain consistent re-

spects from the patterns found in neighboring populations (Fig. 1). The term "dialect" seems appropriate for the properties of the song patterns that characterize each separate population of breeding birds. The detailed structure of syllables in the second part of the song is the most reliable indicator. Such dialects are known in other song birds (3).

The white-crowned sparrow is remarkable for the homogeneity of song patterns in one area. As a result the differences in song patterns between populations are ideal subjects for study of the developmental basis of behavior. If young male birds are taken from a given area, an accurate prediction can be made about several properties of the songs that would have developed if they had been left in their natural environment. Thus there is a firm frame of reference with which to com-

pare vocal patterns developing under experimental conditions. Since 1959 we have raised some 88 white-crowned sparrows in various types of acoustical environments and observed the effects upon their vocal behavior. Here we report on the adult song patterns of 35 such experimental male birds. The several types of acoustical chamber in which they were raised will be described elsewhere.

In nature a young male white-crown hears abundant singing from its father and neighbors from 20 to about 100 days after fledging. Then the adults stop singing during the summer molt and during the fall. Singing is resumed again in late winter and early spring, when the young males of the previous year begin to participate. Young males captured between the ages of 30 and 100 days, and raised in pairs in divided acoustical chambers, developed song

patterns in the following spring which matched the dialect of their home area closely. If males were taken as nestlings or fledglings when 3 to 14 days of age and kept as a group in a large soundproof room, the process of song development was very different. Figure 2 shows sound spectrograms of the songs of nine males taken from three different areas and raised as a group. The patterns lack the characteristics of the home dialect. Moreover, some birds from different areas have strikingly similar patterns (*A3*, *B2*, and *C4* in Fig. 2).

Males taken at the same age and individually isolated also developed songs which lacked the dialect characteristics (Fig. 3). Although the dialect properties are absent in such birds isolated in groups or individually, the songs do have some of the species-specific characteristics. The sustained tone in the introduction is generally, though not always, followed by a repetitive series of shorter sounds, with or without a sustained tone at the end. An ornithologist would identify such songs as utterances of a *Zonotrichia* species.

Males of different ages were exposed to recorded sounds played into the acoustical chambers through loudspeakers. One male given an alien dialect (8 minutes of singing per day) from the 3rd to 8th day after hatching, and individually isolated, showed no effects of the training. Thus the early experience as a nestling probably has little specific effect. One of the group-raised isolates was removed at about 1 year of age and given 10 weeks of daily training with an alien dialect in an open cage in the laboratory. His song pattern was unaffected. In general, acoustical experience seems to have no effect on the song pattern after males reach adulthood. Birds taken as fledglings aged from 30 to 100 days were given an alien dialect for a 3-week period, some at about 100 days of age, some at 200, and some at 300 days of age. Only the training at the age of 100 days had a slight effect upon the adult song. The other groups developed accurate versions of the home dialect. Attention is thus focused on the effects of training between the ages of about 10 and 100 days. Two males were placed in individual isolation at 5 and 10 days of age, respectively, and were exposed alternately to the songs of a normal white-crowned sparrow and a bird of a different species. One male was exposed at 6 to 28 days, the other

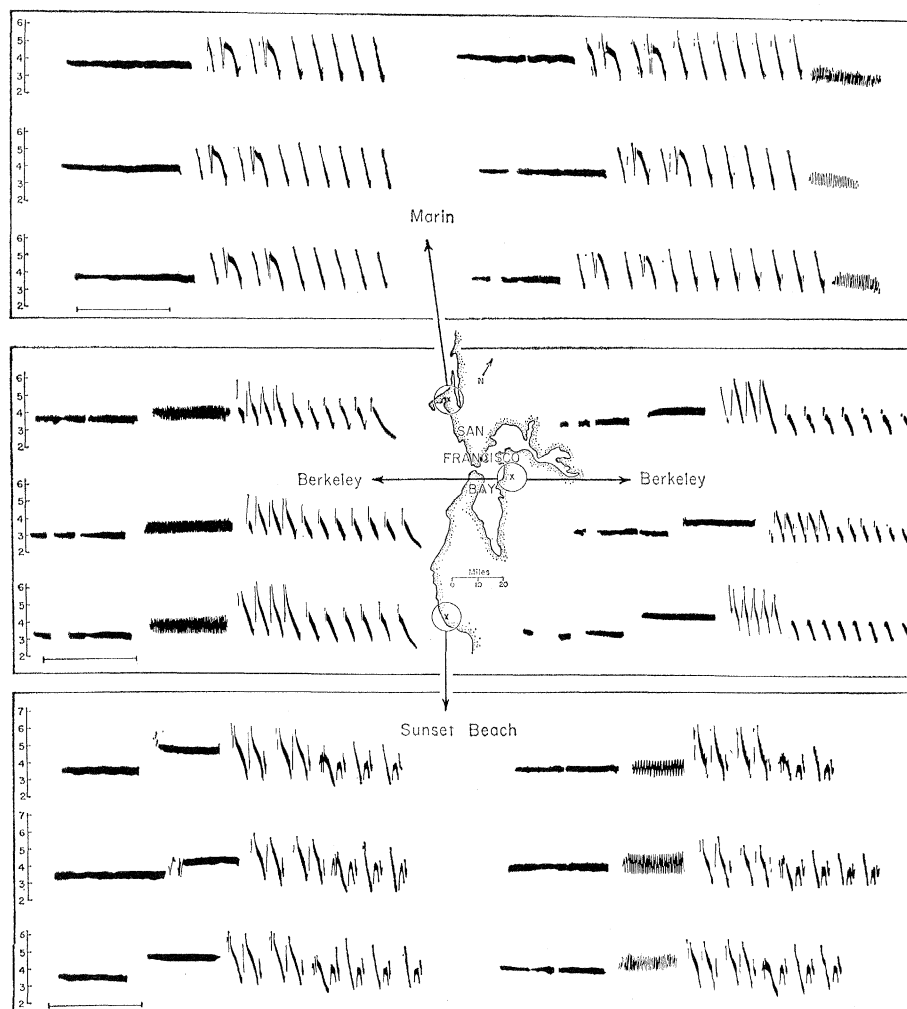


Fig. 1. Sound spectrograms of songs of 18 male white-crowned sparrows from three localities in the San Francisco Bay area. The detailed syllabic structure of the second part of the song varies little within an area but is consistently different between populations. The introductory or terminal whistles and vibrati show more individual variability. The time marker indicates 0.5 second and the vertical scale is marked in kilocycles per second.

at 35 to 56 days. Both developed fair copies of the training song which was the home dialect for one and an alien dialect for the other. Although the rendering of the training song is not perfect, it establishes that the dialect patterns of the male song develop through learning from older birds in the first month or two of life. Experiments are in progress to determine whether longer training periods are necessary for perfect copying of the training pattern.

The training song of the white-crowned sparrow was alternated in one case with the song of a song sparrow, *Melospiza melodia*, a common bird in the areas where the white-crowns were taken, and in the other case with a song of a Harris's sparrow, *Zonotrichia querula*. Neither song seemed to have any effect on the adult patterns of the experimental birds. To pursue this issue further, three males were individually isolated at 5 days of age and trained with song-sparrow song alone from about the 9th to 30th days. The adult songs of these birds bore no resemblance to the training patterns and resembled those of naive birds (Fig. 3). There is thus a predisposition to learn white-crowned sparrow songs in preference to those of other species.

The songs of white-crowned sparrows raised in isolation have some normal characteristics. Recent work by Konishi (4) has shown that a young male must be able to hear his own voice if these properties are to appear. Deafening in youth by removal of the cochlea causes development of quite different songs, with a variable broken pattern and a sibilant tone, lacking the pure whistles of the intact, isolated birds. Furthermore, there is a resemblance between the songs of male white-crowned sparrows deafened in youth and those of another species, *Junco oreganus*, subjected to similar treatment. The songs of intact juncos and white-crowns are quite different. Konishi also finds that males which have been exposed to the dialect of their birthplace during the sensitive period need to hear themselves before the memory trace can be translated into motor activity. Males deafened after exposure to their home dialects during the sensitive period, but before they start to sing themselves, develop songs like those of a deafened naive bird. However, once the adult pattern of singing has become established then deafening has little or no effect upon it. Konishi infers that in the course of

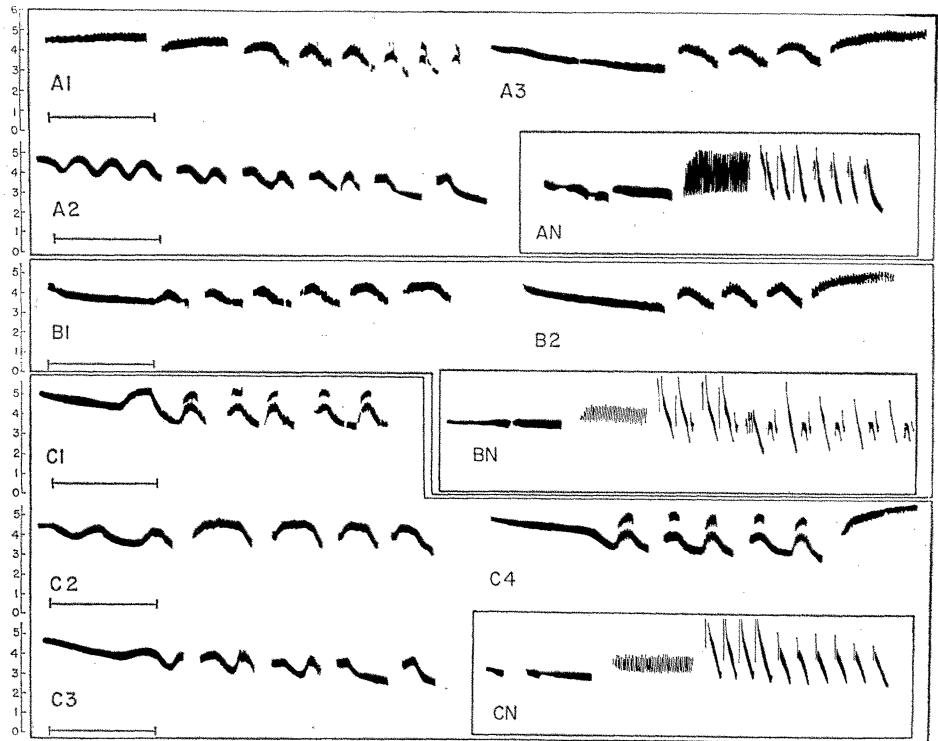


Fig. 2. Songs of nine males from three areas raised together in group isolation. A1 to A3, Songs of individuals born at Inspiration Point, 3 km northeast of Berkeley. B1 and B2, Songs of individuals born at Sunset Beach. C1 to C4, Songs of individuals born in Berkeley. The inserts (AN, BN, and CN) show the home dialect of each group.

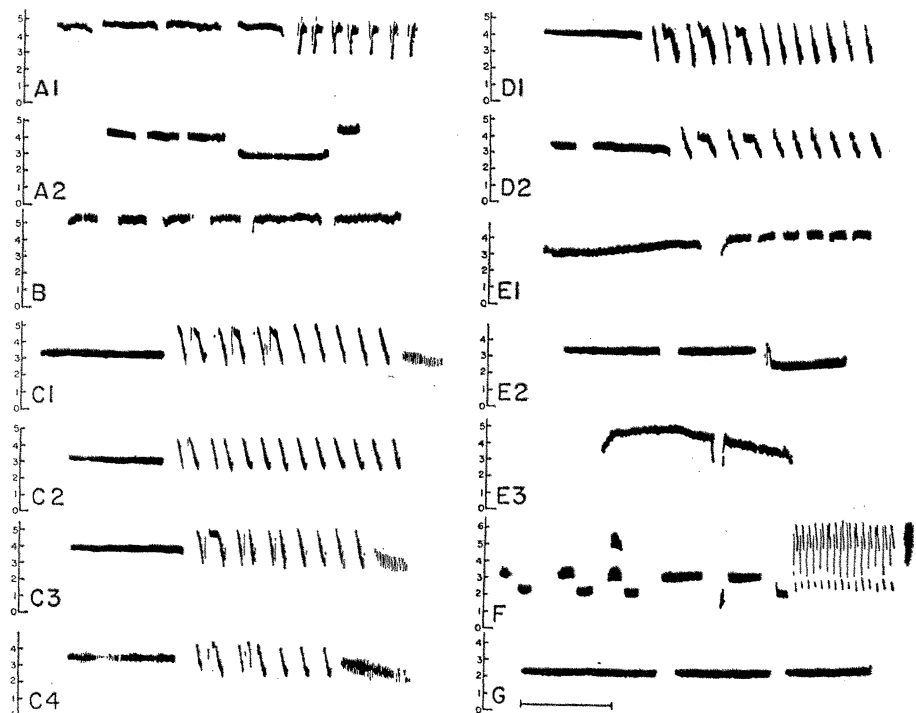


Fig. 3. Songs of 12 males raised under various experimental conditions. A1 and A2, Birds raised in individual isolation. B, Male from Sunset Beach trained with Marin song (see Fig. 1) from the 3rd to the 8th day of age. C1 to C4, Marin birds brought into the laboratory at the age of 30 to 100 days. C1, Untrained. C2 to C4, Trained with Sunset Beach songs; C2 at about 100 days of age, C3 at 200 days, C4 at 300 days. D1, Bird from Sunset Beach trained with Marin white-crowned sparrow song and a Harris's sparrow song (see G) from the age of 35 to 56 days. D2, Marin bird trained with Marin white-crowned sparrow song and a song-sparrow song (see F) from the age of 6 to 28 days. E1 to E3, Two birds from Sunset Beach and one from Berkeley trained with song-sparrow song from the age of 7 to 28 days. F, A song-sparrow training song for D2 and E1 to E3. G, A Harris's sparrow training song for D1.

crystallization of the motor pattern some control mechanism other than auditory feedback takes over and becomes adequate to maintain its organization. There are thus several pathways impinging upon the development of song patterns in the white-crowned sparrow, including acoustical influences from the external environment, acoustical feedback from the bird's own vocalizations, and perhaps nonauditory feedback as well.

Cultural transmission is known to play a role in the development of several types of animal behavior (5). However, most examples consist of the reorientation through experience of motor patterns, the basic organization of which remains little changed. In the development of vocal behavior in the white-crowned sparrow and certain other species of song birds, we find a rare case of drastic reorganization of whole patterns of motor activity through cultural influence (6). The process of acquisition in the white-crowned sparrow is interesting in that, unlike that of some birds (7), it requires no social bond between the young bird and the emitter of the copied sound, such as is postulated as a prerequisite for speech learning in human children (8). The reinforcement process underlying the acquisition of sound patterns transmitted through a loudspeaker is obscure.

PETER MARLER
MIWAKO TAMURA

Department of Zoology,
University of California, Berkeley

References and Notes

1. R. C. Banks, *Univ. Calif. Berkeley Publ. Zool.* **70**, 1 (1964).
2. P. Marler and M. Tamura, *Condor* **64**, 368 (1962).
3. E. A. Armstrong, *A Study of Bird Song* (Oxford Univ. Press, London, 1963).
4. M. Konishi, in preparation.
5. W. Etkin, *Social Behavior and Organization Among Vertebrates* (Univ. of Chicago Press, Chicago, 1964).
6. W. Lanyon, in *Animal Sounds and Communication*, AIBS Publ. No. 7, W. Lanyon and W. Tavolga, Eds. (American Institute of Biological Sciences, Washington, D.C., 1960), p. 321; W. H. Thorpe, *Bird Song. The Biology of Vocal Communication and Expression in Birds* (Cambridge Univ. Press, London, 1961); G. Thielcke, *J. Ornithol.* **102**, 285 (1961); P. Marler, in *Acoustic Behaviour of Animals*, R. G. Busnel, Ed. (Elsevier, Amsterdam, 1964), p. 228.
7. J. Nicolai, *Z. Tierpsychol.* **100**, 93 (1959).
8. O. H. Mowrer, *J. Speech Hearing Disorders* **23**, 143 (1958).
9. M. Konishi, M. Kreith, and J. Mulligan cooperated generously in locating and raising the birds and conducting the experiments. W. Fish and J. Hartshorne gave invaluable aid in design and construction of soundproof boxes. We thank Dr. M. Konishi and Dr. Alden H. Miller for reading and criticizing this manuscript. The work was supported by a grant from the National Science Foundation.

14 September 1964

Mangabey *x* and *b* Wave Electroretinogram Components: Their Dark-Adapted Luminosity Functions

Abstract. *The temporal separation of *x* and *b* components in the electroretinogram of the dark-adapted eye of the sooty mangabey, *Cercocebus torquatus atys*, permits an uncomplicated calculation of luminosity functions. Flicker electroretinogram studies indicate enhancement of the photopic blue sensitivity.*

The electroretinogram (ERG) comprises several individual components which have been treated in great detail by several authors (1-3). Our paper concerns the two major corneal positive components, the *x* and *b* waves. Motokawa and Mita (4) were the first to discover an early positive wave in the response to brief flashes of red light, which they called the *x* wave. In subsequent investigations Adrian (5) showed that the *x* wave had a considerably shorter latency than the *b* wave and was photopic in nature. Armington (6) related the *x* wave to red sensitivity, demonstrating that in man the spectral sensitivity function of the *x* wave fits the CIE (Comm. Intern. de l'Éclairage, ICI) photopic function only in the deep red. The ERG from the dark-adapted primate eye is usually dominated by the *b* component, which has been related to rod function and rhodopsin. The smaller *x* wave can usually be seen in response to flashes of light of long wavelength, but appears, if it can be detected at all, only as a notch in the leading edge of the rising *b* wave at wavelengths shorter than about 590 m μ . However, the ERG of the dark-adapted eye of the sooty mangabey, *Cercocebus torquatus atys*, reveals a distinct separation of the *x* and *b* components of the response at all wavelengths; this permits direct determination of the spectral sensitivity of both components.

The four adult mangabeys used in this study were lightly anesthetized and placed in a stereotaxic instrument. A silver-silver chloride ring electrode was placed around the limbus of each eye. The left eye was covered and the right pupil was dilated with a 1 percent solution of cyclopentolate hydrochloride; the lids were retracted. The animal was placed in a light-tight, electrically shielded box and aligned in the optical system in a manner that placed the final lens focus on the node of the eye, presenting the animal with

a Maxwellian view subtending about 20 degrees of visual angle.

The light source was a 6-volt, 18-amp tungsten ribbon filament bulb. The filament image was condensed and focused on a point aperture. The diverging beam from the point source was collimated, passed through appropriate filters, and then refocused on the node of the animal's eye. An electrically operated flag-shutter interrupted the beam at the point aperture. Flickering light with a light-to-dark ratio of 1:1 was provided by inserting at the aperture an episcope driven by a constant-speed motor. Various combinations of disks and motors provided any desired flicker rate from 2 to 35 cy/sec. Single-flash studies were conducted, with a stimulus duration of 200 msec. Interstimulus intervals were 1 minute or greater, depending on the intensity series. Light composed of narrow-band wavelengths was provided by interference filters or Wratten color filters. Flash intensity was controlled with neutral-density filters. All filters were calibrated with a spectrophotometer and equated for equal energy transmission in the construction of luminosity curves. The filters used gave test flashes at eight spectral points with peak band pass at 452, 490, 505, 538, 576, 606, 633, and 646 m μ .

The ERG was displayed on four

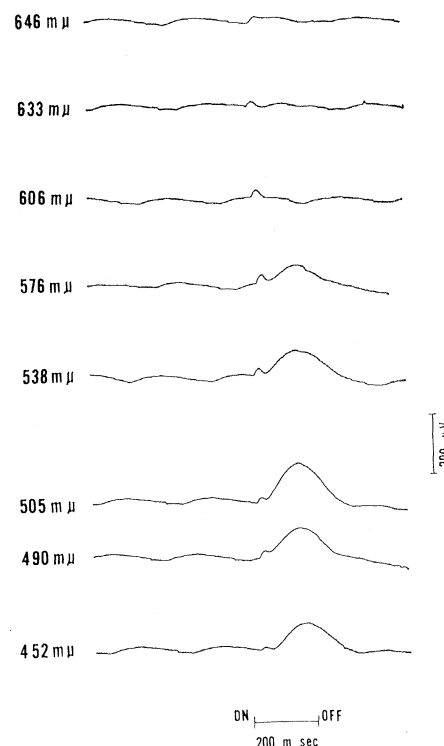


Fig. 1. Electroretinogram of the dark-adapted mangabey eye to a series of equal energy stimuli; animal No. 2.