Photopic Spectral Sensitivity in the Monkey: Methods for Determining, and Initial Results

Abstract. *Data were obtained on the spectral sensitivity of the light-adapted monkey by two operant conditioning techniques adapted to use with brief duration stimuli: cued avoidance conditioning, and a positive reinforcement–reaction time method. The results are compared with human photopic spectral sensitivity, and detailed similarities are found.*

Procedures for obtaining psychophysical data from animals (*1*) are not easily adapted for use with brief stimulus presentations. Since many psychophysical functions are dependent upon a temporal as well as an intensive parameter, it was desirable to develop procedures which would allow for experimental control of the former. Toward this end (i) a modified cued avoidance procedure was developed in which the cue was the stimulus under investigation, and the avoidance response served to indicate that the cue was above threshold, and (ii) a procedure used to obtain animal reaction time was modified so that a short reaction time to the stimulus being investigated indicated that the stimulus was above threshold. These techniques have been applied to determine accurately the foveal, photopic spectral sensitivity of the rhesus monkey as a first step in a series of studies on primate color vision.

The subjects were three male and two female rhesus monkeys, approximately 18 months old. The optical system enabled projection of a narrow band (5 nm half-power) monochromatic spot of light which could be varied in size, brightness, wavelength, and duration. The view provided the subject was Newtonian and monocular, and no special attempt was made to control fixation. A 2-deg or 45-minute test spot was located in the center of a uniformly lit 20-deg field of 3000 trolands (*2*).

In the cued avoidance procedure, subjects were restrained in a commercial primate chair (Foringer No. 1206). The height and position of the chair were adjusted with respect to the eyetube so that the test spot of illumination was directly in the subject's line-of-sight when facing straight ahead. The subject's feet were restrained in aluminum shoes which served as electrodes for an aversive electric shock from a constant-current source designed to deliver a 5-ma, 100-msec impulse.

The test stimulus was a 100-msec flash at random temporal intervals; distribution in time was geometric, and the probability of a flash at the end of each 2-second interval was 0.5. Initially, the subjects were exposed to 200 flashes per session at these random intervals. Sessions typically lasted 2 to 3 hours with one session per day. A shock occurred 2 seconds after each test flash unless the subject pressed a lever in the interim. The subjects, however, learned to avoid almost all shocks by responding at a steady rate, with a mean interresponse time less than 2 seconds. After 8 days, the procedure was modified so that avoidance was possible only if there were no responses in the 2 seconds before the test flash; a 4-second minimum interval was established between flashes. This procedure continued for 25 days before any psychophysical data were taken. During this time, the wavelength and energy of the test flash were varied unsystematically to ensure that the subject would generalize to all wavelengths. The wavelength-energy combinations were all well above threshold for human observers.

Psychophysical data were obtained with a modified method of limits and 20 wavelengths between 420 and 700 nm. One of the extreme wavelengths was selected, and the monkey was subjected to a series of flashes of progressively decreasing intensity until it no longer gave successful avoidance responses. Once threshold, defined as that level of intensity at which the monkey received three shocks in a row, was established, a new wavelength (the next in order toward the other extreme) was employed and the procedure repeated. Only one threshold was determined for each wavelength during any session. Because, in our experience, day-to-day variability in the shape of the relative sensitivity function is less than day-to-day variability in the threshold for a particular wavelength (that

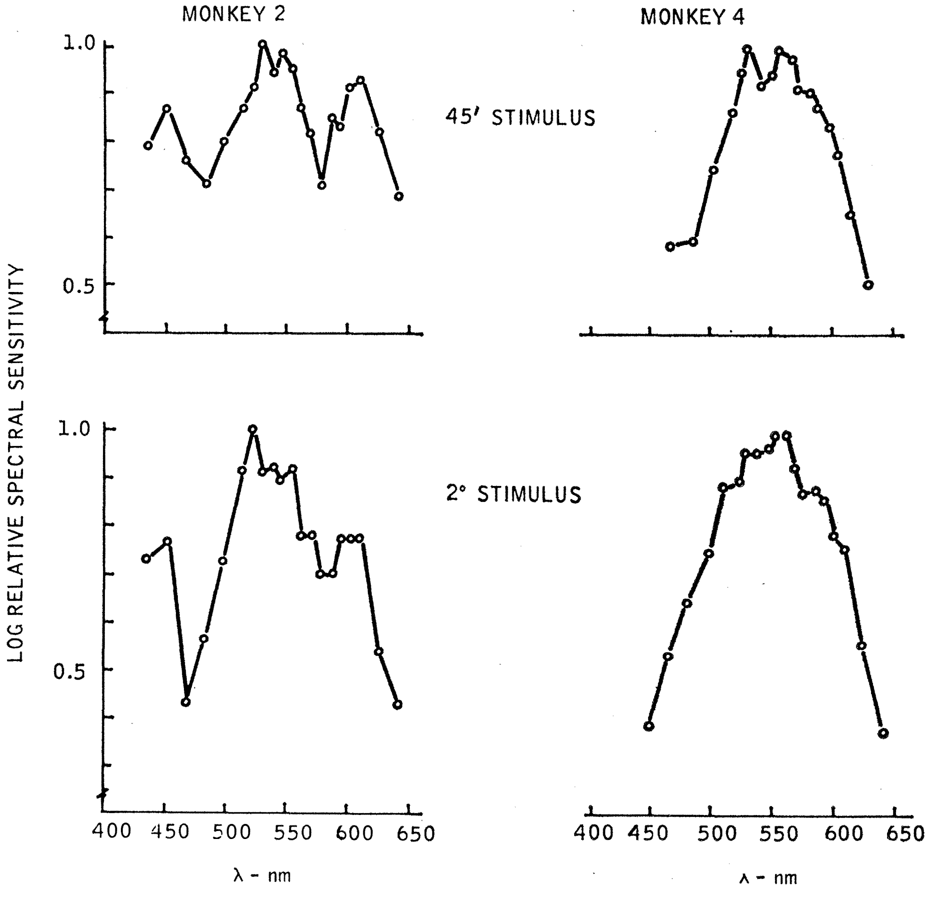


Fig. 1. Relative spectral sensitivity as a function of wavelength for two test stimuli centered in a 20-deg circular surround of 3000 trolands, 2854°K, white adapting light.

is, the absolute position of the sensitivity function), we obtained a relative sensitivity function with less precision each day rather than locate the threshold for only a few wavelengths with greater precision.

Figure 1 presents data on two subjects trained with the cued avoidance procedure. These data are very similar to human data reported by Sperling (*3*). Several characteristics of these spectral sensitivity curves, which have been previously documented for human vision, are: (i) both animals showed a main peak in the 530- to 570-nm region; (ii) monkey No. 2 showed additional peaks in the 450-nm region and in the 610-nm region; (iii) both animals showed dips in the sensitivity curves in the 580-nm region; (iv) the main details of the functions persisted for repeated sessions with the same animal for both test stimulus diameters.

Although the data in Fig. 1 are highly satisfactory in their general form and repeatability, a long-term avoidance response to the entire situation apparently developed. As the animals became increasingly difficult to manipulate, it was decided to develop a positive reinforcement technique which would be simple to implement and easy to learn, and would provide for presentation of brief stimuli.

In the modified reaction-time procedure the subjects were positioned in the chair as in the avoidance procedure, minus the feet restraints. A drinking tube (for reinforcement) positioned in front of the subject permitted alignment of the subject's eye with the artificial pupil when the subject's mouth was in contact with the tube.

The subjects were deprived of water for at least 20 hours prior to each session. They were initially trained to respond for reinforcement (approximately 2 ml of reconstituted orange juice) by depressing and releasing a lever only in the presence of a 1000-cy/sec tone. Responses in the absence of the tone postponed onset of the tone by 10 seconds. After this initial training, the subjects were taught to hold the lever down for longer periods of time before releasing in order to receive reinforcement. The procedure was then modified by introducing the test stimulus (2-deg light spot centered in the 20-deg, 3000-troland surround) while the subject was depressing the lever. The test stimuli stayed on until the lever was released, at which time the light spot and tone terminated and the orange juice was delivered. When the subjects had learned to release the lever in the presence of the light spot, the light was presented as a 100-msec flash, and the subject was required to release the lever within 2 seconds of onset of the flash in order to receive reinforcement. The 2-second requirement was gradually reduced to 622 msec, and the subject's latency stabilized around 350 msec. When the subject failed to release the lever within 622 msec after the flash, the tone was terminated and the 10-second silent period was resumed. To ensure that the subjects would not learn a temporal discrimination anticipating the flash, flashes were scheduled to occur at random following a lever press. The probability of a flash occurring at the end of each 1-second interval following lever depression was 0.3.

From 30 to 40 two- to three-hour sessions, one per day, were needed to reach the flash presentation stage; another 15 to 20 sessions were required before data were taken.

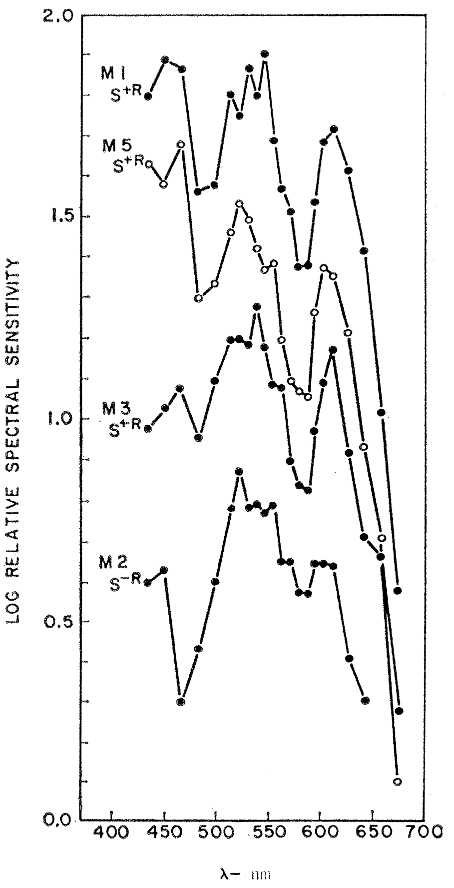
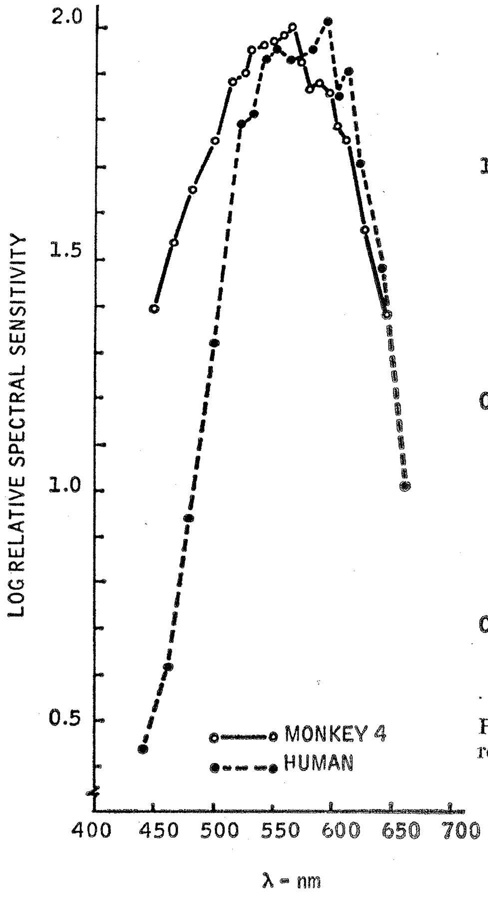


Fig. 2. Relative spectral sensitivity as a function of wavelength for both positive (S^{+R}) and negative (S^{-R}) reinforcement procedures.



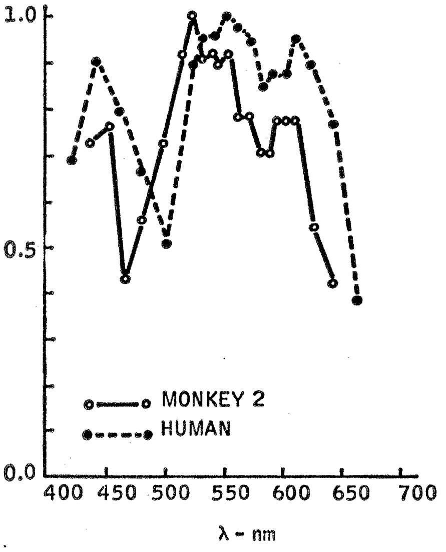


Fig. 3. Comparison of monkey and human relative spectral sensitivity functions.

Data were taken with a modified method of limits and the same stimulus values as in the avoidance procedure. The subjects were presented with a series of flashes at a given wavelength starting at a subthreshold intensity. Successive flashes were intensified unless the subject saw a given flash, at which time those trial conditions were repeated. If the subject released the lever before a flash was presented, that trial was repeated. Threshold was taken to be that intensity at which the subject indicated (by responding to the flash within 622 msec) that he saw two successive flashes.

Figure 2 compares complete spectral sensitivity functions obtained by this technique (designated S^{+R}) on three monkeys (M1, M3, M5), with the one previously obtained (M2) using cued avoidance. It is apparent that essentially the same function was obtained by both techniques. This figure also indicates that the peak found near 610 nm and the deep cleft at 580 nm are probably characteristic of the photopic spectral sensitivity of these primates. Monkey M4 was the only one of five monkeys not showing these features. It is interesting to note that M4 shows a peak at 580 to 590 nm, which is most prominent for the 2-deg field condition (Fig. 1). It may be noted in Fig. 1 that a slight shoulder shows up at 610 nm for M4 which corresponds to the large peak found there with all the other animals. Data on humans obtained with 1000-troland adaptation shows peaks at 580 to 590 nm and at 600 to 610 nm. These rarely appear as distinctly as those of monkeys 1, 2, 3, and 5; rather, in human data, they frequently appear as shoulders or slight humps. In Fig. 3, data obtained for a human subject with a similar-sized, white-light surround and 2-deg test field show the similarities in these features between M2 and M4 and humans. The two human curves were obtained on the same observer at two different luminances of the adapting field—1000 and 10,000 trolands. The M2 data, as well as the data for the other three animals of Fig. 2, agree favorably with the human function for the higher adapting luminance.

The M4 data (Fig. 3) agree in surprising detail with the human adapted to the lower luminance. A possible explanation for the difference between M4 and other monkeys is that M4 has much greater light absorption in the preretinal pigment, making the 3000-troland surround effectively dimmer.

Spectral sensitivity data on a single rhesus monkey obtained by Grether (*4*), in an early experiment on absolute thresholds, show the deep cleft near 580 nm and the secondary peak at 610 to 620 nm. Recent data on the rhesus monkey reported by De Valois (*5*) do not show these features. It is believed, however, that measurements in the latter study were made at too few wavelengths to permit conclusions on the presence or absence of the features reported here. Several studies have shown the dip at 580 nm in humans (*3*).

In addition to demonstrating the usefulness of the two procedures described, these data, although incomplete, show a similarity between monkey and man which may eventually support the conclusion that rhesus monkeys and man have identical mechanisms of spectral sensitivity. While both procedures yield satisfactory data and require about the same investment in time and apparatus, the positive reinforcement paradigm has the additional advantage of keeping the subjects more cooperative.

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2. Trolands were used in order to compare data with those obtained on human subjects. The surround was calibrated with a MacBeth illuminometer 3 inches from the ground glass positioned in front of the final lens and artificial pupil. The average luminance of several readings was 48 mlam. With the formula $T = 10 \cdot B \cdot r^2$, where T = trolands, B = the brightness in millilamberts (48 for our surround), and r = the radius of the limiting pupil (in this case, animal's pupil taken to be 2.5 mm), the surround was calculated to be 3000 trolands. The relative radiant energy of the 2-deg test spot was measured at the pupil of the eye with a platinum-black, compensated thermocouple. The attenuation of the continuous-density filter, used to vary luminance of the test spot, was measured with the thermocouple over two log units at 35 wave bands in the region from 380 to 720 nm.
3. H. G. Sperling, *Federation Proc.*, Suppl. 14, **24**, 573–577 (1965); *Vision Res.* **1**, 42 (1961); ———, and C. L. Jolliffe, *Science* **136**, 317 (1962).
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5. R. L. De Valois, "Behavioral and electrophysiological studies of primate vision," in *Contributions to Sensory Physiology*, W. D. Neff, Ed. (Academic Press, New York, in press).
6. Supported by the U.S. Army Medical Research and Development Command under contract No. DA-49-193-MD2457.

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Communication between Dolphins in Separate Tanks by Way of an Electronic Acoustic Link

Abstract. *Two isolated dolphins* (Tursiops truncatus) *were provided with an electronic acoustic link during alternate periods of approximately 2 minutes. The dolphins repeatedly communicated in a tight sequence when the acoustic link was connected. Their responses varied as the experiment progressed. Some information regarding possible meaning of the whistles was obtained.*

Dolphins emit a variety of sounds underwater that include whistles, click trains, and miscellaneous signals. The complexity and extent of dolphin communication are not known. The click trains are used for echolocation (*1, 2*); the whistles correlate with evident communication and variations in behavior and emotional state (*1, 3–5*). Miscellaneous signals appear during feeding, sexual activity, and playing (*3*). Dreher (*6*) reported considerable vocal response by a group of six dolphins (*Tursiops truncatus*) to each of six different recorded dolphin whistles. Lilly (*7*) reported that *Tursiops* can match numbers and durations of human vocal bursts. Lilly and Miller (*8*) physically restrained each of two dolphins at opposite ends of a tank of water using visual barriers that still permitted them to hear each other and to reply. The animals emitted numerous sounds in sequenced exchanges with but few superpositions. Each dolphin

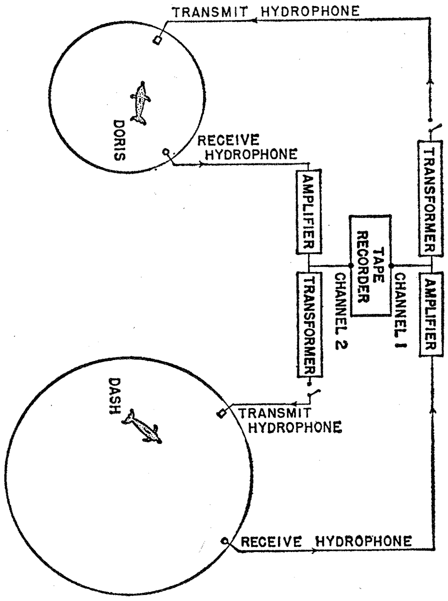

Fig. 1 Diagram of intertank communication test.