J Comp Physiol A (1985) 157:247–253

Journal of Comparative Physiology A Sensory, Neural, and Behavioral Physiology

Spectral sensitivity of the African cichlid fish, *Haplochromis burtoni*

Ethan E. Allen and Russell D. Fernald
Institute of Neuroscience, University of Oregon, Eugene, Oregon 97403, USA

Accepted April 22, 1985

Summary. Spectral sensitivity of the cichlid fish *Haplochromis burtoni* was measured under both scotopic and photopic conditions using a two-choice, food reward, operant conditioning paradigm. The highest absolute sensitivity (scotopic) is one quantum for every 5 to 50 rods measured at 475 nm (equivalent to a corneal irradiance of 3.8×10^6 Q s^{-1} cm^{-2}). A $P500_1$ photopigment apparently mediates spectral sensitivity over most of the visible spectrum; microspectrophotometric studies of rods had previously shown them to contain this photopigment. However, the scotopic behavioral action spectrum shows a sensitivity to short wavelength light higher than is consistent with a $P500_1$ photopigment alone mediating the scotopic visual process. Determinations made under photopic conditions reveal a behavioral action spectrum broader than that found under scotopic conditions and consistent with mediation by interaction of the three known cone types in an opponent processing manner. The calculated photopic threshold value of approximately 10^4 Q s^{-1} $(\text{receptor})^{-1}$ is in agreement with results from other species and corresponds to a corneal irradiance of about 7×10^{10} Q s^{-1} cm^{-2}.

Introduction

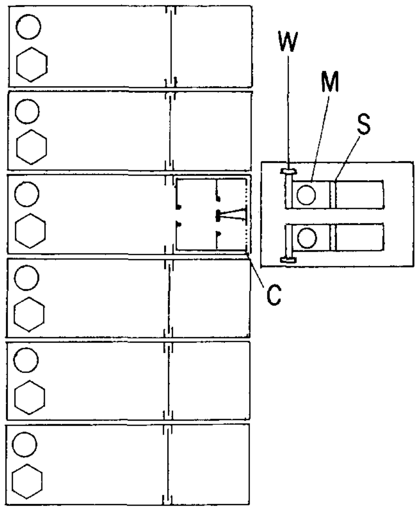
The African cichlid fish, *Haplochromis burtoni*, in which most encounters among individuals are mediated by vision (Fernald 1977; Fernald and Hirata 1977a, b), possesses a duplex retina with one type of rod and both single and morphologically twin cones. The cones are arranged in a 'square' mosaic pattern characteristic of highly visual teleosts (Fernald 1981). Microspectrophotometric (MSP) measurement has revealed that the single cones, which are physically shorter than the twins, contain the visual pigment $P455_1$ while within each pair of twins one cone contains $P523_1$ and the other contains $P565_1$ (Fernald and Liebman 1980). The arrangement of the cone pigment pairs maximizes the uniformity and density of packing and may also optimize the ability to detect chromatic boundaries (Fernald 1981). The rods, whose density is constant over the extent of the retina (Fernald 1983), contain the visual pigment $P500_1$ (Fernald and Liebman 1980) and are intercalated into the cone matrix in a ratio of between 1 and 2 rods to each cone. Cone density is not uniform, being higher in the vicinity of the temporal pole of the retina than in other areas (Fernald 1983). Evidence from microspectrophotometric measurements after bleaching individual photoreceptors suggests that they contain only a vitamin A_1-based photopigment (Fernald and Liebman 1980).

The present study reports the spectral sensitivity functions obtained from intact, freely-moving individual animals under both scotopic and photopic conditions. Preliminary accounts of some of these results have been presented (Allen and Fernald 1981, 1982, 1983).

Materials and methods

Subjects and living conditions. Adult male and female *H. burtoni* bred from wild caught animals and weighing between 5 and 13 g were the subjects in the experiments reported here; all lived in the conditions described below for at least one month prior to testing. Subjects were housed individually in seven gallon glass aquaria which were each divided into two sections as shown schematically in Fig. 1A. The tanks of fish were arrayed side by side; male and female fish were arranged alternately so that each had as its nearest neighbors two individuals of the opposite sex, providing the most uniform visual social stimulation possible during daylight hours. A living area contained gravel, a filter, and a shelter (half of a 2 inch flower

A



B

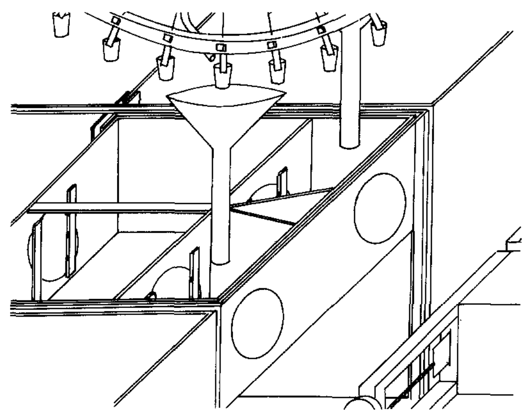


Fig. 1. A Schematic view showing arrangement of tanks, testing chamber (*C*), monochromators (*M*), neutral density wedges (*W*), and shutters (*S*). **B** Enlarged view of testing chamber, illustrating the feeders, targets, and infrared sensors at the chamber entrances (imbedded in vertical strips)

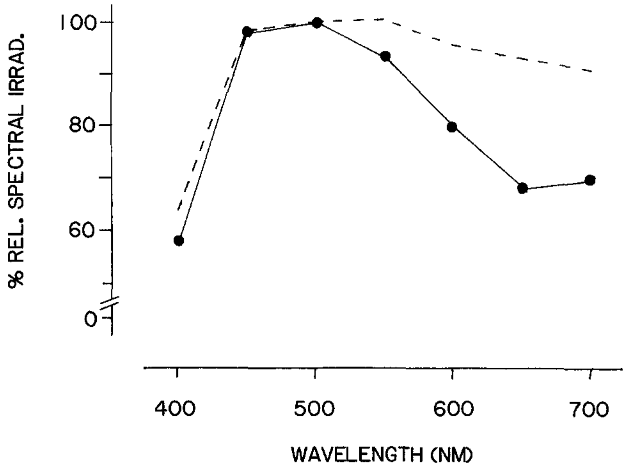


Fig. 2. Spectra of daylight [sunlight plus skylight (from Judd et al. 1964); dashed line] and the filtered incandescent source used in the photopic experiments reported here (solid line). Ordinate is in units of Q; abscissa in nm

pot); the testing area (kept closed off from the living area except during test sessions) held the testing chamber itself, shown in Fig. 1B. This apparatus had three divisions; a main chamber was separated from the two target chambers by a nearly transparent acrylic divider (a completely transparent divider proved confusing to the fish when they attempted to swim through it; lightly sanding the transparent acrylic barrier allowed passage of most of the available light yet made it visible to the fish). Entrances between chambers measured 2.5 × 5 cm (Fig. 1B). A pH of 8.2–8.9 was maintained by the addition of Tanganyika salts (Mesco, Inc.); tank temperature was regulated at 23–26 °C (Fernald and Hirata 1977b). Food was available only in the testing chamber.

All animals were maintained on a 12:12 L:D cycle throughout these experiments and all testing was done during the middle four hours of their dark or light phase to ensure full dark or light adaptation. Although these fish are normally diurnal, they readily learned to perform the task required at night in order to obtain food. During the scotopic experiments the background illuminant in the light phase of the L:D cycle was provided by four 40 W fluorescent tubes suspended 20 cm above the tanks; this source provided a background daytime illuminant of 3×10^{10} Q s^{-1} cm^{-2} nm^{-1} in its peak region between 525 and 625 nm, when measured 2 cm beneath the surface of the water (using a Gamma photometer model 2400 with 700-31 monochromator). During testing (in the dark phase of the L:D cycle) these lights were off. During the photopic experiments, care was taken to provide a light regime which was as spectrally similar to that encountered in the wild state as was possible. Suspended 10 cm above each tank was a 100 W frosted tungsten-filament incandescent bulb filtered to convert the relatively red-biased tungsten light to a more nearly spectrally flat illuminant characteristic of sunlight/skylight (C.I.E. source C; filters were Kodak Wratten 78AA; cf. Wyszecki and Stiles 1967). The spectrum from this source is shown as the solid line in Fig. 2 as measured (Gamma photometer model 2400 with model 700-31 monochromator) 3 cm under the surface of the water directly beneath the opening of the light housing; the spectrum of daylight (from Judd et al. 1964) is shown for comparison (dashed line). This source provided 6.3×10^8 Q s^{-1} cm^{-2} over the range of 450–550 nm. This light source was on during photopic testing.

Training and testing. An operant conditioning paradigm employing a two-choice, food reward (live or frozen brine shrimp (*Artemia*)) design was used throughout the tests. Early training, conducted during the dark phase of the L:D cycle, consisted of shaping each subject's feeding behavior so as to develop an association between food and an illuminated target; long intervals between stimulus presentation and subject response were allowed, but, as learning progressed, the interval was shortened to 10 s. Ten to fifteen sessions of training generally sufficed to bring subjects to consistent levels of at least 80% correct performance.

A trial was initiated when the subject passed through an infrared beam (G.E. matched emitter-detector pairs # H23B1; peak output at 940 nm, with no output below 800 nm) at the entrance to the main testing chamber. The electrical signal thus generated latched a high frequency (1,000 Hz) oscillator into one of two states, thus selecting randomly either the right or