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Eye movements in the African cichlid fish, *Haplochromis burtoni*

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Summary. 1. There are three distinct kinds of coordinated eye-body movements in the African cichlid fish, *Haplochromis burtoni*, as revealed by cinematographic analysis: a) eye movements without coordinated body movements (voluntary saccades); b) nystagmus consisting of compensatory eye movements during turning of the body and a reset saccade movement of the eyes; c) fast body turns executed without corresponding eye movements.

2. During voluntary scanning eye movements the eyes usually move in temporal synchrony and often the result is a decreased angle between the eyes (increased convergence of the eyes).

3. Compensatory eye movements produce successive fixation of the gaze direction during a slow rotation of the body which serve to maintain the angular orientation of the eyes in space. No systematic change in convergence is associated with these turns.

4. Fast body turns are very rapid body turns without compensatory eye movements which occur almost exclusively during social interactions.

5. When the animals are freely swimming, these three types of eye-body movements occur in all possible sequences.

Introduction

Eye movements in vertebrates have a variety of functions. For example, when the body position is changed by rotation, the image of the world on the retina can be maintained approximately constant by eye movements of the opposite sense. Such compensatory eye movements are found in a wide range of vertebrate visual systems and are presumed to ease the task of seeing while moving (Walls 1967). These compensatory eye movements, which appear nearly automatic when an animal is in motion, can be contrasted with voluntary eye movements which an animal uses to direct its gaze at objects of interest within its visual field. In particular, animals with specialized retinal regions containing high concentrations of retinal photoreceptors in an area centralis or fovea generally direct their eyes so that objects of interest form an image on that area. The rapid positional shifts between points of eye fixation are termed saccadic movements (Dodge 1903).

Fish move almost continuously throughout their lives and fish eye movements are frequent and obvious, particularly in species for which vision is a dominant sensory modality. While in motion, fish actively maintain their orientation with respect to various cues in the environment including water flow, gravity (von Holst 1950a), light (von Holst 1950b), other animals and reference points both on the substrate and in the water. As the fish moves, its eyes also move so that different portions of the visual world are sampled successively. In a typical teleost, each eye subtends a visual field covering approximately 180–190° of solid angle (Trevarthen 1968; Easter et al. 1977; Fernald et al. in preparation). Since fish have lateral eyes, the visual fields of their two eyes together cover a great extent of the visual world. There is only a small caudal blind area of 10 to 15° wherein lie the trunk and the tail of the fish (Fernald et al. in prep.). Active movement through space considerably increases the visual information a fish must process in order to correctly interpret its visual world, since displacement of points in the visual field relative to the eyes results in transformation

Abbreviations: BO body; *CF* compensation factor; *LE* left eye; *RE* right eye

of the visual image by relocation on the retina. Eye movements are probably very important in stabilizing these images on the retinae.

We have analyzed the horizontal eye movements in the African cichlid fish, *Haplochromis burtoni*. This animal is particularly suited for such an analysis because it depends on vision to recognize a highly complex and sophisticated set of behavioral signals which mediate social interactions (Fernald 1977, 1984). Territorial males have spatial and chromatic patterns on their bodies which they can turn on and off quickly to communicate behavioral intent and motivational state. It has been shown that these signals are critically important for the animal both in aquaria (Fernald 1977) and in their natural environment (Fernald and Hirata 1977a, b). Walls (1962) predicted that fish which are highly visual in their orientation will show particularly sophisticated adaptations in their eye movements. *H. burtoni* appears to be a candidate for just such sophistication and therefore a systematic investigation of eye movements was undertaken.

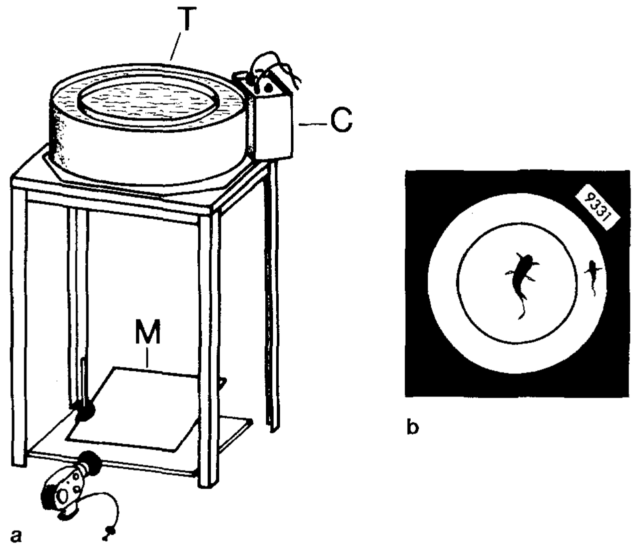

Fig. 1. Left: Schematic illustration of the observation tank (*T*) held so that it could be filmed from below via a front surface mirror (*M*). The electronic counter (*C*) was positioned so that its face was included in filmed image, allowing identification of individual frames and calibration of film speed. Right: Sketch of the image on the film where the central fish has eye stalks to allow eye movements to be observed and measured

Methods

Data acquisition. Mature male *H. burtoni* (7.0 to 7.5 cm long) were fitted with stalks on their eyes to allow measurement of eye movements. The eye stalks were made from black electronic 'shrink' tubing (0.5 mm diameter × 4.0 mm) by squeezing one end closed with heated tweezers and then chewing gently on the tubes for a few minutes to soften them so that they could be attached by suction to the caudal edge of the fishes' cornea. The obstruction of the visual field was 10% or less and the estimated viscous drag was not significant. Fish with eye stalks were placed in a cylindrical plexiglas tank (50 cm diameter and 15 cm high) with a transparent floor (Fig. 1). The outer circumference was covered with uniformly opaque material and the tank illuminated from above through a translucent cover to eliminate external visual cues. From 1 to 5 fish with eye stalks were filmed from below with the image reflected in a front surface mirror. Filming was done on super 8 mm film at 60 frames/s. An electronic counter driven by a pulse generator at known frequency was filmed simultaneously to allow identification of individual frames as well as for calibration of film speed (see Fig. 1).

Data analysis. Film segments ($n = 185$) containing eye or body movements were projected frame by frame and the angular position of each of the two eye stalks and the body were measured as shown schematically in Fig. 2. Each frame was viewed through a clear plexiglas disk etched with parallel lines which were then aligned parallel to the object of interest, either an eye stalk or the body axis by an observer rotating the disk. A digital potentiometer produced a voltage proportional to the angle of the disk selected, and this value was coded on paper tape to be read by computer (DEC 11/40). The orientation of the body and of each eye of the fish was thus measured with respect to the tank for each frame. This angular measurement was repeatable with an accuracy of $\pm 1°$. The body axis was taken as the line perpendicular to a line drawn between the two eyes (Fig. 2a).

To compute the magnitude of the saccadic eye movements, the angular position before an saccade was subtracted from the angular position afterwards using the mean value of eye position for five sample points (film frames) just before onset of the eye movement and just after the end of the eye movement respectively. The 'vergence', or relative convergence of the eyes was computed by calculating a mean angle between the eyes at rest for sample periods, and comparing it with the angle between the eyes measured before and after a shift in gaze.

Three different presentations of these data are shown here. First, the absolute angular position of the eyes and body are plotted as a function of time (cf. Fig. 3a). The abbreviations of LE for left eye, BO for body and RE for right eye are used throughout. Second, the angular position of the eyes relative to the body are plotted as a function of time (see Fig. 4b). The relative position of the left eye is denoted LE-BO, that of the right eye, RE-BO and the relative position of the two eyes, LE-RE. Third, the position of the eyes relative to one another are plotted on orthogonal axes so that any point on the plane corresponds to a unique angular relationship among the two eyes and the body (Figs. 2c, 3b, 4c, 7).

The plots of relative eye position contain considerable information about eye movements which is not easily obtained from other representations. Each frame of the film is represented by a point on the plot corresponding to the relative angle of the two eyes with respect to the body as measured in that frame. The points are connected in the temporal sequence in which they occurred, and arrows represent movement of time. Thus each eye movement is a 'trajectory' in the plot, where the line connecting two successive measured positions corresponds to a single frame of film (ca. 16 ms). The length of the line thus corresponds directly to angular velocity of the eye movements so that longer lines mean higher velocities. Points above the abscissa correspond to movements of the right eye towards the nose and these below to movements of the