Control of a teleost social signal

I. Neural basis for differential expression of a color pattern

Linda E. Muske* and Russell D. Fernald

Institute of Neuroscience, University of Oregon, Eugene, Oregon 97403, USA

Accepted July 14, 1986

Summary. Territorial male Haplochromis burtoni (Teleostei; Cichlidae) have a dark facial stripe, the 'eyebar', which can appear and disappear within seconds, independently of other coloration patterns. It is used to signal territory ownership and aggressive intent. Some males, called 'barless', have functional melanophores in the eyebar region but never display this pattern, because melanin in eybar pigment cells is never dispersed.

The eybar melanophores are controlled by a specialized branch of the maxillary nerve. Lesioning the 'eyebar nerve' resulted in immediate melanin dispersion and consequent darkening of the eybar pattern, and it abolished the normal paling response in all behavioral situations. Nerve lesion produced similar results in both barred and barless males, except that the coloration of the denervated eybar in barless males was more similar to camouflage markings than to the conspicuous black eybar used as a social signal.

Electrical stimulation of the maxillary nerve produced melanin aggregation. Photoelectric recordings of this paling response revealed no differences between barred and barless males, or between the eybar and other facial chromatophores that do not function as visual displays. Thus, the difference in the physiological state of eybar melanophores in intact barred and barless males cannot be explained by differences in peripheral nerve anatomy or physiology.

Introduction

The ability to change color in response to different environmental or social cues is a nearly universal characteristic of fishes. While color change in elasmobranchs and lampreys is limited to relatively slow, uniform darkening or lightening, controlled by hormones (Waring 1963), most evolutionarily advanced teleosts are able to produce a striking array of color patterns that serve a variety of diverse functions. Superimposed on endocrine mechanisms, neural control of color change, which can be virtually instantaneous, is most well developed in teleosts. Some markings are cryptic, others are bright and conspicuous. Color patterns used for 'advertisement' are especially common among highly visual, social teleosts, and behavioral studies indicate that many such patterns function as intraspecific signals, to attract mates, signal aggressive intent or communicate with young (reviewed by Fine et al. 1977). In this and in a related study (Muske and Fernald 1987) we report on the physiological control of a conspicuous melanophore pattern, used as a social signal by adult male Haplochromis burtoni, and on peripheral specializations not previously described which appear to be involved in both its development and expression.

Color change in cold-blooded vertebrates is produced by specialized pigment cells known as 'chromatophores'. There are several types of chromatophores, classified according to the pigment they contain. Pigment granules are motile, and it is the dispersion or aggregation of pigment within the chromatophore that causes the skin to change color. Based on speed of response, the 'instantaneous' changes characteristic of many social chromatophore signals are thought to be entirely under neural (sympathetic) control. However, this hypothesis has not been critically tested, as previous studies of chromatophore physiology have focused almost exclusively on background adaptation, a process in which the skin darkens or lightens more or less uniformly when the luminance of the environment is changed (cf. Healey 1951; Gray 1956;...
Pye 1964). It is believed that the communicatory function of chromatophores evolved secondarily from background adaptation (Baerends 1976). Since interpretation of social signals is essential for the smooth functioning of animal societies, it would not be surprising to find that corresponding to the change in function, specializations have arisen to enhance the visibility of the signal and to ensure that its expression occurs within an appropriate social and motivational context.

The African cichlid *H. burtoni* is an excellent subject for testing hypotheses about regulation of social chromatophore signals. This species inhabits shallow pools at the shore of Lake Tanganyika and exhibits complex, visually guided social behavioral patterns. Correspondingly, the fish display a variety of color patterns characteristic of sex, social status and motivation. In particular, territorial (breeding) males display a prominent dark stripe beneath the eye ('eyebar') which is known to influence aggressive behavior in other males (Leong 1969; Heiligenberg et al. 1972). Recognition of the eyebar appears to be innate, as it is observed in males raised in complete isolation (Fernald 1980). Eyebar expression is highly correlated with dominance and aggression. Disappearance of the bar is common in situations of fear or flight (Fernald 1977) and the eyebar, alone of the territorial color patterns, can appear and disappear within seconds, independently of other markings.

Some males successfully defend a territory but never display an eyebar (Fig. 1). These 'barless' males have the same pigment cells in the eyebar region as the more common 'barred' morph, and they will sometimes display a dull, cryptic grey version of the eyebar as part of an over-all camouflage pattern (Muske 1983). However, during aggressive social interactions, in which the 'true' eyebar of barred males is prominently displayed (i.e. melanin granules are dispersed), the pattern is entirely absent in barless males (melanin is fully aggregated). There are no morphs intermediate between barred and barless, and except for the eyebar, barred and barless territorial males appear identical, both behaviorally and morphologically (Fernald 1977; Muske 1983).

The existence of the two color morphs provides a natural opportunity for identifying structures and mechanisms that underlie particular coloration effects produced by dermal chromatophores. In the report that follows (Muske and Fernald 1987) we show that specific physiological differences characterize eyebar pigment cells of barred and barless males, and that anatomical specializations are present in barred territorial males which enhance conspicuousness of the display. In the present study, we wanted to know: (1) How is eyebar darkening controlled in barred males? (2) Are there neurological differences between barred and barless males that account for the differences in the activity of their eyebar melanophores?

**Methods**

We performed two types of experiments on chromatic-motor nerves to analyze control of the eyebar: (1) nerve lesioning followed by observational studies, to identify the neural input to the color pattern and (2) electrical stimulation of chromatophore nerves, to compare pigment cell response in barred and barless males.

*Nerve lesion studies.* All experimental subjects were taken from stable laboratory colonies in aquaria containing 10 to 20 reproductively active adults, including two or more territorial males (see Fernald 1977 for a detailed description of the social organization and behavior of *H. burtoni*).