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# Sonic and electric fish: At the crossroads of neuroethology and behavioral neuroendocrinology

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**Abstract**

Field and laboratory studies of weakly electric and sound-producing teleost fishes demonstrate how steroidal and non-steroidal hormones mediate the translation of neural events into behavior. The development of this research program has depended upon an interdisciplinary neuroethological approach that has characterized the neurophysiological properties of the motor and sensory pathways that lead to the production and detection of easily quantified highly stereotyped behaviors, namely, electric organ discharges (EODs) and vocalizations. Neuroethological studies of these teleosts have now integrated a behavioral neuroendocrinology approach that has provided several examples of how hormone-sensitive neurobiological traits contribute to adaptive behavioral plasticity in natural habitats. As such, these studies provide guideposts for comparable studies in other groups of teleosts and vertebrates in general.


*Keywords:* Electrogenesis; Electroreception; Vocalization; Audition; Androgens; Estrogen; Glucocorticoids; Teleost fish

## Introduction

The major premise of this review is that field studies that integrate the disciplinary approaches of neuroethology and behavioral neuroendocrinology guide the initial recognition and subsequent investigation of behaviorally relevant hormone-dependent plasticity in neural systems. Studies of weakly electric fish and sound-producing fish provide examples of how the actions of steroidal and non-steroidal hormones on individual neurons and neural systems lead to modifications in behavior. The sensory and motor systems of teleosts that govern the detection and production of electric organ discharges (EODs) and vocalizations are well defined and involve relatively few groups of neurons dedicated to these behaviors. These studies were also among the first to show how hormones modulate the neurophysiological mechanisms of social behaviors in teleost fishes and vertebrates in general. Since recent comprehensive reviews of these model systems are available elsewhere (e.g., Bass and McKibben, 2003; Rose, 2004), we will first provide a brief historical context for current studies of electric and sonic fish and then highlight the contributions of the most recent studies showing how hormones act as dynamic modulators of neural systems and behavior. In so doing, we hope to both inspire and challenge others (and ourselves!) to employ multiple levels of analysis to delineate the neuroendocrinological events that contribute to adaptive behavioral plasticity.

Teleost fishes show a range of reproductive tactics that are perhaps greater than any other vertebrate group (see Taborsky, 1994). This includes species that show behavioral switches from male to female tactics (and vice versa) within a matter of minutes to those that show more gradual changes in their reproductive phenotype over periods of days and years. While studies of sonic fish have provided some important demonstrations of the neurophysiological basis of reproductive plasticity (see later section), investigations in a wide range of other teleosts have demonstrated a dynamic

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relationship between changing neuropeptide phenotypes in the preoptic area and anterior hypothalamus and transformations in either male social status and/or male reproductive displays (for recent reviews, see Bass and Grober, 2001; Grober and Bass, 2002). The companion paper by Oliviera on teleost fishes provides some examples of these diverse neural–behavioral phenotypes in teleosts.

## Historical overview

Studies of both electric and sonic fish benefit from a rich history of comparative studies of neural and behavioral mechanisms between closely and distantly related species. The relatively more recent behavioral neuroendocrinology studies of these teleosts rest upon a series of neurophysiological analyses by Michael V. L. Bennett, Theodore H. Bullock and their colleagues working on electric and sonic fish in the United States and Thomas Szabo and his colleagues working on electric fish in France (historical overview: see Bass, 1986; Zakon, 1986 for electric fish; Bass and McKibben, 2003 for sonic fish). Of particular relevance to this review are the intracellular recording studies by Bennett and colleagues that used electric and sonic fish as models of electrotonic coupling in the nervous system (see Bennett, 1971; Pappas and Bennett, 1966). During the 1970s, the use of autoradiographic techniques led to the identification of hormone-concentrating cells within the central nervous system of a broad range of vertebrates, including teleost fish (Morrell et al., 1975). These studies included the discovery of steroid-concentrating neurons within the vocal motor systems of songbirds and anuran amphibians (Arnold et al., 1976; Kelley, 1980). Thus, the potential for direct steroid action on neurons was extended from the hypothalamic–pituitary axis of the brain to motor systems linked to species-typical display behaviors. Against this backdrop of comparative neurophysiological studies on electric and sonic fish and autoradiographic studies across vertebrates in general, field studies of the behavioral biology of electric and sonic fish were entering a growth phase (see Hopkins, 1986 for electric fish; see Tavolga, 1971; Fine et al., 1977 for sonic fish). Together, these studies provided the fuel for the studies we review here.

## Weakly electric fish

In the early 1980s, studies of electric fish began to combine the disciplinary approaches of behavioral endocrinology and cellular neurophysiology. Investigations of the independently evolved weakly electric South American gymnotid fish (Meyer and Zakon, 1982) and African mormyrid fish (Bass and Hopkins, 1983, 1985) showed that androgens could induce an EOD that mimicked naturally occurring sex differences in this signal (Hopkins, 1972, 1980; Bass and Hopkins, 1985), which is in agreement with the higher levels of androgens in field-caught males (Zakon et al., 1991) and with laboratory maintained populations of males in breeding condition (Landsman, 1993; Carlson et al., 2000). These studies suggested that steroids work at multiple levels acting both on the central pattern generator and the electric organ's spike generating cells (electrocytes) as well as in the frequency sensitivity of the electrosensory systems that paralleled shifts in the spectral content of the EOD (Fig. 1).

EOD pulses are longer in duration among males than females in most species, and this pattern has evolved independently in both groups. For example, the EOD is sinusoidal in the South American gymnotiform *Sternopygus*. The neurons in the hindbrain central pattern generator (the pacemaker nucleus) of males fire at a low frequency so that the longer EOD pulses of the male form a sine-wave like discharge, whereas these neurons fire at a high rate in females so that the shorter female pulses maintain a sine-wave like discharge. In addition, the electroreceptors of each fish are best tuned to its own EOD frequency to aid in electrolocation. Systemic androgen treatment of females or juvenile fish masculinizes the electrosensory and motor systems: it simultaneously lowers the pacemaker firing frequency, broadens the electric organ pulse duration and lowers the tuning of the electroreceptors to the new EOD frequency over 1–2 weeks (Meyer and Zakon, 1982; Zakon and Meyer, 1983; Meyer, 1983; Keller et al., 1986; Mills and Zakon, 1987, 1991) (Fig. 1). Conversely, estrogen treatment causes physiological changes in the opposite direction as androgens, that is, it feminizes the electrosensory and motor systems (Dunlap et al., 1997). Comparable studies of the unrelated African mormyrid fish that generate a pulsatile EOD similarly show that androgen-induced increases in EOD pulse duration and spectral content are paralleled by decreases in electroreceptor tuning (Bass and Hopkins, 1984).

## Coordination of androgen-dependent changes

The electroreceptors, pacemaker neurons and electrocytes are three different cell types with quite different intrinsic electric properties whose behaviors are tightly co-regulated by androgens. This raises a question about whether androgens act directly at a single target site, e.g., the pacemaker nucleus, which then indirectly affects changes at the other sites, or whether androgens act directly and independently at all three sites. In *Sternopygus*, androgens retune the electroreceptors in fish in which the electric field has been eliminated by spinal section or following pacemaker nucleus lesions, which removes the electric field as well as any possible calibration signals from the brain (Keller et al., 1986; Ferrari and Zakon, 1989). On the output side, microimplants of androgens directly in the