MECHANISMS IN THE PHOTOPERIODIC CONTROL OF REPRODUCTION IN THE STICKLEBACK

by

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Summary

In sticklebacks, sexual maturation is stimulated by long photoperiods but not by short photoperiods, even at high temperatures. Extra-retinal photoreception can mediate this response, and appears to be more important than retinal photoreception. Although plasma melatonin levels are high at night and low during the day, experiments using melatonin administration via the water indicate that melatonin is of no or little importance for the photoperiodic response. Androgens can be aromatised to estrogens in the stickleback brain. Treatment with aromatase inhibitors stimulates maturation of males also under short photoperiod, suggesting that aromatase is involved in the suppressive actions of short photoperiod. Expression of both follicle stimulating hormone (FSH)-β and luteinizing hormone (LH)-β is higher under long than under short photoperiod. FSH-β is controlled by a negative steroid feedback on the brain-pituitary-gonad axis under short photoperiod and by a positive steroid feedback under long photoperiod. It is suggested that the former can suppress reproduction under short photoperiod and the latter can stimulate breeding under long photoperiod.

Keywords: Photoperiod, stickleback, reproduction, photoreceptors, melatonin, aromatase.

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Introduction

In almost all animals living in temperate regions, reproduction is a seasonal event. In order to produce offspring at a time when the chance of survival is highest, animals need to sense environmental cues telling them what season it is. The most important external cue is the photoperiod, although other environmental factors such as temperature are also involved in the control of seasonal reproduction. Some fishes like cyprinids and sticklebacks spawn when days are lengthening in spring-summer (long-day breeders), whereas others, such as most salmonids, spawn in autumn-winter when days are shortening (short-day breeders). In both cases, numerous experimental studies have demonstrated effects of photoperiod on the timing of reproduction (e.g. Dutton & Bromage, 1987; Awaji & Hanyu, 1988). It is now well established that reproduction in the three-spined stickleback, *Gasterosteus aculeatus*, can be controlled by photoperiod manipulation (e.g. Baggerman, 1957; Borg, 1982a), with sexual maturation being stimulated by long photoperiods, and inhibited by short photoperiods. The present article reviews the mechanisms by which photoperiodic effects on stickleback reproduction are mediated.

Photoreceptor organs

In order to influence reproduction, photic information needs to be detected by photoreceptors. In mammals, the presence of photoreceptors is only clearly established in the eyes. In contrast, in most non-mammalian vertebrates extra-retinal photoreceptors are also present, the most recognised of these being in the pineal organ (Ekström & Meissl, 1997). The pineal organ is not directly photosensitive in mammals, but in fishes, including the stickleback (van Veen *et al.*, 1980), it contains well-defined photoreceptor cells, structurally similar to those found in the retina. In addition, deep encephalic photoreception is known from many vertebrates, and photoreceptors can also be present in the parapineal organ and in the skin. Benoit (1964) observed that extra-retinal photoreceptors can mediate photoperiodic effects on reproduction in birds, as blinded ducks can be stimulated to mature by long photoperiods. Mediation of photoperiodic effects by extra-retinal photoreceptors has been observed in many animals, including sticklebacks (Borg, 1982b). Menaker *et al.* (1970) demonstrated that when the roof of the skull of sparrows is shielded so that light is prevented from reaching the encephalic pho-