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Review

Molecular mechanism of the photoperiodic response of gonads in birds and mammals☆

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Abstract

Appropriate timing of various seasonal processes is crucial to the survival and reproductive success of animals living in temperate regions. When seasonally breeding animals are subjected to annual changes in day length, dramatic changes in neuroendocrine–gonadal activity take place. However, the molecular mechanism underlying the photoperiodic response of gonads remains unknown for all living organisms. It is well known that a circadian clock is somehow involved in the regulation of photoperiodism. Recently, rhythmic expression of circadian clock genes was observed in the mediobasal hypothalamus (MBH) of Japanese quail. The MBH is believed to be the center for photoperiodism. In addition, long-day-induced hormone conversion of the prohormone thyroxine (T_4) to the bioactive triiodothyronine (T_3) by deiodinase in the MBH has been proven to be important to the photoperiodic response of the gonads. Although the regulating mechanism for the photoperiodic response of gonads in birds and mammals has long been considered to be quite different, the long-day-induced expression of the deiodinase gene in the hamster hypothalamus suggests the existence of a conserved regulatory mechanism in avian and mammalian photoperiodism.

Keywords: Circadian clock; Deiodinase; Japanese quail; Photoperiodism; Thyroid hormone; Median eminence; GnRH; Mediobasal hypothalamus; Hamster

Contents

1. Introduction

In most animals living in temperate regions, reproduction is under photoperiodic control. This ensures the birth of young in spring or summer, the optimal seasons for survival. In most seasonal breeders, testicular size increases during the breeding

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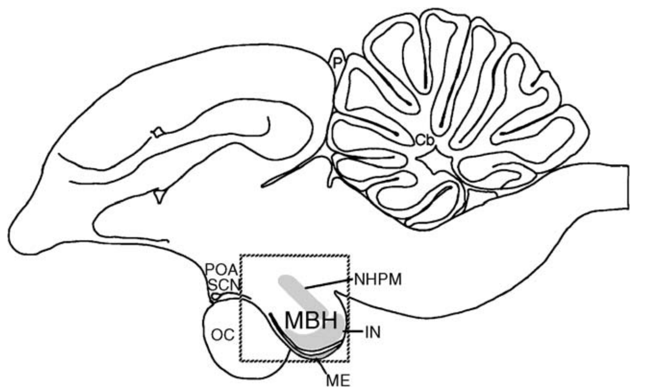

Fig. 1. The mediobasal hypothalamus (MBH) of Japanese quail. Cb: cerebellum; IN: infundibular nucleus; ME: median eminence; NHPM: nucleus hypothalamicus posterior medialis; OC: optic chiasm; POA: preoptic area; SCN: suprachiasmatic nucleus; P: pineal gland.

season and decreases during the non-breeding season. These differences are more pronounced in birds than in mammals, probably because of avian adaptations for flight. Most small mammals and birds with a short gestation or egg-laying period breed during spring and summer, and are so-called long-day breeders. In contrast, animals that have gestation periods of ~6 months breed during fall and are so-called short-day breeders. In mammals, photoperiodic information is translated into a daily cycle of melatonin from the pineal gland, and the duration of the night is reflected in the length of the nocturnal melatonin secretion. In long-day breeders, short-day-induced melatonin suppresses gonadal activity, while it induces gonadal activity in short-day breeders such as the sheep and goat (Arendt, 1995). In spite of the distinct role of melatonin in seasonal reproduction in mammals, the down-stream events dependent on melatonin action remain unknown. Although melatonin has a determining role in regulating photoperiodic response of gonads in mammals, no effect of melatonin manipulation is observed in the seasonal regulation of gonads in birds (Gwinner et al., 1997). In addition, birds have extraocular photoreceptors in the brain linked to the photoperiodic response of the gonads, while the eye is the only organ to mediate photoperiodic response in mammals (i.e., enucleation abolishes photoperiodic response in mammals, while it has little effect in birds) (Benoit, 1935a,b; Menaker, 1968; Menaker et al., 1970). The reasons for these differences between avian and mammalian photoperiodism had been a mystery for several decades.

2. Photoperiodic response in birds

Among the various avian species, Japanese quail is known to be an excellent model system for the investigation of photoperiodism because of its rapid and dramatic response to photoperiod (Follett et al., 1998). Therefore, a considerable number of studies have been made of Japanese quail over the past few decades. Reproduction of vertebrates is regulated by the hypothalamic–pituitary–gonadal (HPG) axis. Activity of gonads is regulated by the gonadotropin (LH and FSH) secreted from the pituitary gland and gonadotropin release is under the control of gonadotropin releasing hormone (GnRH) secreted from the hypothalamus. Numerous reports have suggested that the mediobasal hypothalamus (MBH), including the infundibular nucleus (IN), the median eminence (ME) and nucleus hypothalamicus posterior medialis (NHPM) is an important center for the regulation of photoperiodism in birds (Fig. 1). For example, lesions of the IN, the ME, or NHPM within the MBH can block the rise of LH and testicular growth under long photoperiods (Sharp and Follett, 1969; Davies and Follett, 1975a; Ohta and Homma, 1987). In a lesion study, blocking of the photoperiodic response is effective even though the GnRH system has been left intact (Juss, 1993). In addition, electrical stimulation of IN increases LH secretion (Konishi et al., 1987) and induces testicular growth (Ohta et al., 1984). Furthermore, the expression of Fos-like immunoreactivity in IN and ME has been shown to result from the photostimulation of one long-day photoperiod (Meddle and Follett, 1995, 1997). In addition to these reports, deep brain photoreceptors are thought to be localized in the IN (Silver et al., 1988).

3. Involvement of the circadian clock in photoperiodism

It is an established fact that the circadian clock is involved in the photoperiodism of various organisms (Pittendrigh, 1972). In quail, it has been clearly shown that light pulses at a specific time of day, called the photoinducible phase, are effective for photoperiodic induction (Follett and Sharp, 1969; Yasuo et al., 2004a) (Fig. 2). The photoinducible phase lies early in the subjective night (i.e., ~10–16 h from dawn). Although the photoperiodic clock of quail seems to be a damping or weakly self-sustaining oscillator when compared with other avian species such as the white crowned sparrow and blackheaded bunting, night-break experiments and Nanda–Hamner experiments suggest that it is indeed based on a circadian rhythm (Saiovici et al., 1987; Follett et al., 1992). Circadian (~24 h) rhythms are a fundamental property of living systems and impose a 24 h temporal organization regulating the physiology and biochemistry of most organisms. The intracellular clock mechanism is composed of interacting positive and negative transcriptional feedback loops that drive ~24 h rhythms in the RNA and protein levels of key clock

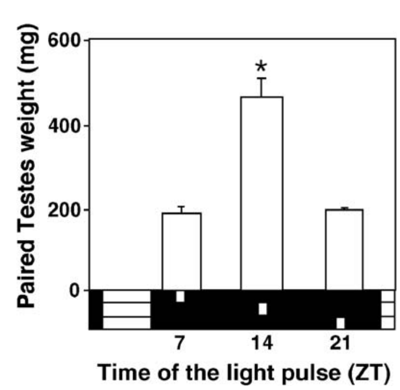

Fig. 2. Light pulses at photoinducible phase cause testicular growth. In each group, animals were given light pulses for 10 days. Asterisk: one-way ANOVA, Fisher's LSD post-hoc test, $P<0.01$ (modified from Yasuo et al., 2003).