



Photoperiodic regulation of reproduction in birds

Ila Mishra

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Abstract

Birds time their activities in synchronization with daily and seasonal periodicities in the environment, which is mainly provided by changes in day length (=photoperiod). Photoreceptor cells in an avian brain are localized in three independent neural structures, the retina of eyes, pineal gland and hypothalamus. Deep brain photoreceptors (DBPs) localised particularly in the paraventricular organ (PVO) and lateral septal area (LSO) of hypothalamus are implicated in regulation of photoperiod induced reproductive response. DBPs relay the photoperiodic information to the pars tuberalis thyroid hormone stimulating (TSH) expressing cells. The TSH mediated signalling mediates the photoperiod induced gonadotropins releasing hormone (GnRH) release from the pre optic area (POA). In addition to the GnRH, other neurohormones including the neuropeptides Y (NPY), vasoactive intestinal peptide (VIP), and the neurosteroids, especially the brain derived testosterone contribute to regulation of the overt reproductive response and behaviour in seasonal breeding avian species. Here, we briefly review limited evidence on the roles of photoreceptors, and the local hormone variations of the hypothalamus in the regulation of seasonal physiology, particularly in the long-day breeding species.

Key Words: avian, breeding, photoperiodic

Introduction

Adaptation to the environment that a species inhabits is of crucial importance. This is clearly reflected in adaptation for breeding which in most, if not all, species occurs when food resources in the surrounding are optimal and adequate to provide nourishment to the young ones. This is an absolute requirement, failing which will greatly compromise breeding success of the population and may endanger the species. In the wild, the 'favourable' time (season) for breeding is ensured by variables in the environment. For this reason, many mammals have evolved with a period of gestation in their reproduction. Mammals with a long gestation period such as goat, sheep and horses give birth to the young ones in times extending from winters to early-spring, while those with short gestation period like rodents, dogs and ferrets give birth mostly during the summer months. In birds, the breeding patterns are very diverse, depending on the environment a species inhabits. At mid- and high-latitudes, the annual breeding cycle in most, if not all, birds are governed by an annual photoperiodic cycle or simply phased or synchronized by it. This is because at these latitudes, the most conspicuous

and reliable environmental periodicity is the annual change in day length (= photoperiod). Compared to this, at lower latitudes where annual photoperiodic cycle is of the low amplitude, the environmental factors other than the photoperiod become important regulators of the breeding seasons. Most seasonal species of birds use annual photoperiod variation as cue, which they internally decode to determine the length of the day (hence night) and perhaps thus seasons (Bradstaetter et al., 2000; Kumar, 1997; Kumar and Follett, 1993; Kumar et al., 2007). Changes in day length (photoperiod) acts as a primary cue in regulation of seasonal cycles of reproduction, molt and migration (Cassone and Yoshimura, 2015; Kumar, 1997, Kumar et al., 2010). There are extensive investigations, and photoperiodic regulation of reproduction has been shown in many species irrespective of the inhabiting latitudes (Follett, 1984; Kumar et al., 2010; Wingfield and Farner, 1993). Because, the annual photoperiod cycles do not vary year-to-year, the breeding time in such species is highly predictable. In subtropics, for example, long day breeding species inhabiting India, like the Indian weaver bird, *Ploceus philippinus*, and subtropical tree sparrow, *Passer montanus*, begin their

Author's Address

Department of Zoology, University of Delhi, Delhi-110007
E-mail: ilamishra90@gmail.com



breeding season with the gonadal recrudescence in response to increasing day lengths of the late spring and summer, but end the breeding season with gonadal regression later in the summer when daylight is still longer in duration than those were photostimulatory during late spring (Chandola et al., 1975; Rani et al., 2007). These species are called photosensitive (or more commonly photoperiodic) birds, and selectively respond to the annual photoperiodic cycle (to increasing or decreasing photoperiods). This is not surprising since light seems to have played a definitive role in the evolution of most, if not all species.

Thyroid-mediated transduction of photoperiodic response

Photoperiod-induced changes in seasonal physiology and behaviour are associated with changes in the circulating hormone levels, in particular the sex steroids such as testosterone and estradiol hormones that regulate the overt metabolic responses including the thyroid hormones (Goodson et al., 2005; Ramenofsky, 2011). Thyroid hormones are involved in the long-day photostimulation (Cassone and Yoshimura, 2015) of reproductive responses in seasonal birds and mammals. On the other hand, elevated circulating sex steroids, in particular the testosterone levels have been found to be associated with socio-sexual behaviours such as aggression, mating, solicitation and singing during the reproductively active phase in many birds (Ball and Balthazart, 2002; Goodson et al., 2005). Long-day induction of photoperiodic response begins with the photoperception by the deep brain photoreceptors. Photoreceptors are light sensing opsin containing cells that are coupled to a chromophore derived from an 11-cis form of vitamin A retinaldehyde, which is capable of phototransduction. Light absorbed by photoreceptors photoisomerizes the 11-cis retinaldehyde to all-trans retinaldehyde. This conversion of 11-cis to all-trans induces a conformational change in the opsin molecules and initiates the phototransduction cascade via activation of the downstream signalling proteins (Wald, 1968). Unlike mammals, where only eyes are the photoreceptive structure, birds possess photoreceptive function in at least 3 tissues – eyes, pineal and hypothalamus. However, these multiple photoreceptive structures do not independently

regulate the photoperiod induced responses. It is largely proposed that they interact with one another to regulate the circadian and/or seasonal timing in birds, albeit the relative contribution varying with species and also possibly with seasons of the year (see reviews Cassone and Menaker, 1984; Gwinner et al., 1997; Gwinner and Brandstätter, 2001; Kumar and Singh, 2006). Further, experimental evidences suggest that photoreceptors in the hypothalamus, called the deep brain photoreceptors (DBPs) play a critical role in regulation of the photoperiod induced reproductive responses. The first evidence for the presence of DBPs came from the experiments done on *Europena minnows* (*Phoxinus laevis*) in 1911 by Karl von Frisch. An absence of both eyes and pineal gland did not interfere with the light-induced changes in skin colour in minnows. The first evidence of role of DBPs in regulation of photoperiodic induction of gonadal response came from Frisch's study on ducks (*Anas platyrhynchos*) in 1935. In this study, placing a black cap on the head of ducks blocked the access of light to brain tissue and thus, did not induce the long-day mediated gonadal stimulation. Thereafter, many studies on bilaterally enucleated birds also suggested an active participation of extraretinal photoreceptors in controlling the reproductive responses to changes in day length in Japanese quail (*Coturnix japonica*), chicken (*Gallus gallus*), house sparrows (*Passer domesticus*), white-crowned sparrows (*Zonotrichia leucophrys gambelii*) and ducks (Oishi et al., 1966; Menaker, 1968; Menaker and Keatts, 1968; Harrison and Becker, 1969; Ookawa, 1970a,b; Gwinner et al., 1971; Harrison, 1972). Until recently, many DBPs have been identified in various species of photoperiodic birds, including rhodopsin, melanopsin, neuropsin and vertebrate ancient (VA) opsin. Neuropsin (also called opn 5) expressed in CSF-contacting neurons and VA-opsin expressed in the anterior and medial hypothalamus have been linked to the photoreceptor mediated neuroendocrine signalling that regulates the seasonal breeding responses in birds (Halford et al., 2009; Nakane et al., 2010). As proposed by Nakane et al. (2010), information about the photoperiodic environment is detected by the Opn5 neurons in the PVO and translated via G protein-coupled receptor into a biological action into the external zone of the ME, juxtaposed to pars tuberalis, PT, which is the



site of thyroid stimulating hormone-beta subunit, Tsh- β release. Thus, it is suggested that a highly conserved thyroid hormone-responsive molecular mechanism of the pars tuberalis mediates photostimulation of gonadal growth and development (see reviews Cassone and Yoshimura, 2015; Nakane and Yoshimura, 2014; Surbhi and Kumar, 2014). Photostimulation begins with the concurrent activation of *eya3* (*eye absent 3*) and *tsh β* (thyroid stimulating hormone-beta subunit) genes in the pars tuberalis (PT) thyrotrophs (Majumdar et al., 2014; Nakao et al., 2008). Under a stimulatory photoperiod, thyroid stimulating hormone (TSH- a protein product of TSH α and TSH β) released from PT thyrotrophs activates and suppresses the transcription of genes coding for type 2 and 3 deiodinases (*dio2* and *dio3*) in tanycytes lining the third ventricle, which mediate the conversion of T4 (thyroxine) into active T3 (triiodothyronine, biologically active form) and rT3 (reverse T3, biologically inactive form), respectively. T3 regulates the synthesis and/or release of GnRH (gonadotropin releasing hormone) from the preoptic area into the median eminence, and consequently the secretion of pituitary gonadotropins (Cassone and Yoshimura, 2015; Nakane and Yoshimura, 2014). Further, intracerebroventricular (ICV) injection of TSH has been shown to mimic the long-day induced *Dio2* expression in the tanycytes, further corroborating the suggested role of Tsh β as an endocrine regulator of avian seasonal reproduction (Nakao et al., 2008). Further, enhanced local hypothalamic levels of T3 causes morphological changes in the glial-neuron interactions at the level of gonadotropin-releasing hormone (GnRH; a hypothalamic peptide) nerve terminals in the median eminence and thus control the GnRH secretion from the preoptic area, POA, into the hypophyseal portal system (Yoshimura et al., 2003; Yamamura et al., 2004).

Thyroid hormone mediated seasonal plasticity of GnRH neurons

Immunoelectron microscopy of ME of Japanese quails revealed the GnRH neuro-glial plasticity modulated GnRH secretion when birds were transferred from short to long days. In short days, the endfeet of glial cells totally encapsulate the GnRH nerve terminals, thus retraining the contact

between GnRH nerve terminals and basal lamina, the site of GnRH release. However, on exposure to long days, T3 binds to the glial endfeet to bring about morphological changes in its structure, causing a retraction of glial endfeet. This enables a close proximity between GnRH nerve terminals and basal lamina, which results in stimulation of gonadotropins secretion by the pituitary (Yamamura et al., 2004). Hypothalamic GnRH release stimulates synthesis and secretion of anterior pituitary gonadostimulatory hormones viz. luteinizing hormone (LH) and follicle stimulating hormone (FSH). LH and FSH act on the target reproductive tissues and induce gonadal growth and thus the production of steroid hormones, viz. testosterone and estrogen (Ball, 1993; Wingfield and Farner, 1993). Based on localization in the brain, GnRH is recognized in two forms, GnRH-I found expressed in the preoptic area (POA), and GnRH-II found expressed in the midbrain (Perfito et al., 2011). It is suggested that GnRH-I regulates the pituitary gonadotropin secretion and thus facilitates seasonal timing of reproduction (Dawson et al., 2015). Increasing evidences also show species variation in hypothalamic GnRH content in relation to the annual reproduction among seasonally breeding birds. There is an increase in GnRH immunoreactivity (-ir) in POA (preoptic area) in response to increasing daylengths with peak during the breeding season, and this is followed by spontaneous decline with regression and photorefractoriness in absolute photorefractory species like the American tree sparrows (*Spizella arborea*; Reinert and Wilson, 1996), European starlings (*Sturnus vulgaris*; Foster et al., 1987), house sparrows (*Passer domesticus*; Hahn and Ball, 1995), dark eyed Juncos (*Junco hyemalis*; Meddle et al., 2006), and redheaded buntings (*Emberiza bruniceps*; Surbhi et al., 2016). There can be differences in the expression pattern of GnRH-I between species showing absolute and relative photorefractoriness in their photoinduced gonadal growth-involution cycle (Surbhi et al., 2015, 2016). GnRH-II, on the other hand, is a non-hypophysiotropic peptide system and present in a rather conserved sequence in the midbrain area lying posterior to the third ventricle. Evidences suggest that GnRH-II does not play a major role in pituitary regulation of reproduction in birds (Meddle et al., 2006). Evidences suggest the role of



GnRH-II in the regulation of reproduction-associated behaviours in birds, independent of the GnRH-I (Maney et al., 1997; Perfito et al., 2011). Intracerebroventricular (ICV) infusion of cGnRH-II, not cGnRH-I, has been shown to enhance solicitation behaviour in female white-crowned sparrows (Maney et al., 1997). The season- and age-dependent immunoreactivity also suggests the role of GnRH-II in reproduction associated processes in house sparrows (Stevenson and MacDougall-Shackleton, 2005). Interestingly, the reproductive flexibility of the opportunistic breeding birds such as zebra finch is attributed to the tonic activation of GnRH-I with the activation and inactivation of GnRH II in the breeding and non-breeding states, respectively (Perfito et al., 2011).

Other neurohormones involved in photoperiodic responses

Tsutsui and colleagues (2000) discovered GnIH (gonadotropins inhibiting hormone), which was found to express in the hypothalamic paraventricular nucleus (PVN) with projections extending to the median eminence (ME). This peptide has been found to directly inhibit gonadotropin release by the pituitary, mediated by GnIH receptors (Tsutsui et al., 2013). There has been a considerable effort in establishing its role in the regulation of seasonal reproductive cycle via inhibitory effects on the hypothalamic GnRH system and/ or anterior pituitary secretions (Tsutsui et al., 2013). Both, *in vivo* and *in vitro* GnIH administrations have been shown to inhibit the synthesis of *LH-β* and *FSH-β* in the chicken and quail pituitary glands (Ciccone et al., 2004; Ubuka et al., 2006). A direct effect of GnIH on testes response via reduction in the LH/ FSH-stimulated testosterone secretion has also been suggested in house sparrows (*Passer domesticus*; McGuire and Bentley, 2010). Also, a role of hypothalamic GnIH (gonadotropin releasing hormone) in controlling GnRH activity has been suggested in house sparrows, *Passer domesticus*, and European starlings, *Sturnus vulgaris* (Bentley et al., 2003; Ubuka et al., 2008). Further, at the transcriptional level, increased *gnih* mRNA levels in hypothalamic explants from short days, compared to long days, paralleled the significantly reduced plasma LH levels and gonadal size in Japanese quail, *Coturnix*

c. japonica (Chowdhury et al., 2010). In addition to GnRH and GnIH, NPY and VIP play a regulatory role in the seasonal gonadal responses (Surbhi et al., 2015). NPY is known to affect several physiological functions in birds, including the regulation of food intake and energy homeostasis (Richardson et al., 1995), release of GnRH (Contijoch et al., 1993), sexual maturation (Fraley and Kuenzel, 1993), development of secondary sexual characters, such as song behaviour (Fiore et al., 1999). ICV injections of NPY affect testis development in chicken (Fraley and Kuenzel, 1993) and causes preovulatory surge of LH in hens (Contijoch et al., 1993). Further, NPY and GnRH-I neurons are in close association in the POA, IN (infundibular nucleus) and ME in chicken hypothalamus (Kuenzel, 2000). The NPY protein and NPY mRNA are expressed in the POM, IN, ME, PVN, which contain the GnRH and GnIH cells and fibres (Singh et al., 2013). Both anatomical and functional evidence support the role of NPY in avian reproduction. NPY may also exert an indirect regulatory role on reproduction by affecting the feeding and energy homeostasis (Klingerman et al., 2011). Similarly, VIP as a stimulatory factor for tonic secretion of pituitary prolactin regulates post-reproductive behaviours in birds, namely egg production, incubation and feeding of the offsprings (El Halawani et al., 1995, 1996, 1997). Immunoneutralization of VIP increases egg laying and inhibits the incubation behaviour in turkeys, *Meleagris gallopavo* (El Halwani et al., 1995, 1996). Hypothalamic VIP mRNA and protein content of the INc complex (infundibular nucleus, IN and Inferior hypothalamic nucleus, IH) positively correlates with circulating prolactin levels during different reproductive stages in birds (Youngren et al., 1996). The close contacts of VIP with GnRH-I in the lateral septal organ (LSO), septal area (SA) and median eminence (ME) (Teruyama and Beck, 2001), and with opsins in the lateral septum (SL) and infundibular regions (IN; Silver et al., 1988) support the role of VIP in the reproduction and light perception, respectively. Evidence show that VIP induced prolactin secretion suppresses GnRH release (Sharp et al., 1998) and triggers gonadal regression (Youngren et al., 1996; Zadworny et al., 1988), with consequent stimulation of the incubation and nest-protective behaviours in birds (Opel and Proudman, 1989).



Further, in birds, steroids of both neural and peripheral origins are involved in the regulation of changes associated with the gonadal growth-regression cycle (Goodson et al., 2005). In the brain, testosterone (T) can bind directly to its own receptors (androgen receptor, ar) or, after its conversion to 17 β -estradiol by aromatase enzyme (coded by *cyp19* gene), to estrogen receptors, and thereby affect male sexual behaviours, aggression, territoriality, vocalization and other reproductive responses (Goodson et al., 2005; Ramenofsky, 2011). Moreover, there can be species- and season-specific variations in T-driven behaviours attributable to differences in production, conversion to estrogenic metabolites, and/ or dynamics of the androgen/ estrogen receptor sensitivity (Canoine et al., 2007; Hau et al., 2000; Soma et al., 2000). For example, brain androgen receptor and/or aromatase activity regulates aggression during the non-breeding season when circulating T levels are low in song sparrows (*Melospiza melodia*; Soma et al., 2000) and tropical spotted antbirds (*Hylophylax naevioides*; Hau et al., 2000).

Conclusion

Most temperate songbirds are highly dependent on photoperiod changes for their reproductive capabilities. Photoreceptors play a key role in the perception of light and dark signals of the environment. DBPs seem to play a crucial role in regulating the biological clock governed avian physiological processes. Photoperiodic information is perceived by the photoreceptors, and processed in the brain through thyroid-hormone mediated phototransduction pathways that measure the photoperiodic time. Outputs from this pathway control the seasonally appropriate phenotypes by regulating the synthesis and release of hypothalamic gonadotropins releasing hormone and pituitary gonadotropins. The possible connections of avian photoreceptors among themselves and with circadian and photoperiodic systems remain poorly understood. The regulation of overt reproductive physiology and behaviour includes the regulation of aggression, mating behaviour, vocalisations, visual displays, parenting and other social behaviours. Neurosteroids, especially testosterone is a formidable regulator of these reproduction

associated behaviours in seasonally breeding songbirds.

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Ila Mishra

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