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The role of the pineal gland in the photoperiodic control of bird song frequency and repertoire in the house sparrow, *Passer domesticus*

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Highlights

- The passerine song control system contains melatonin receptors, and administration of melatonin affects seasonal song control structure size.
- Is the pineal gland involved in seasonal changes in song behavior?
- In this study, pinealectomy of house sparrows dramatically alters the seasonal responses of house sparrow song behavior in different photoperiods.
- This effect is independent of effects of photoperiod on gonads.
- Seasonal control of birdsong is at least in part due to the pineal gland.

Abstract

Temperate zone birds are highly seasonal in many aspects of their physiology. In mammals, but not in birds, the pineal gland is an important component regulating seasonal patterns of primary gonadal functions. Pineal melatonin in birds instead affects seasonal changes in brain song control structures, suggesting the pineal gland regulates seasonal song behavior. The present study tests the hypothesis that the pineal gland transduces

photoperiodic information to the control of seasonal song behavior to synchronize this important behavior to the appropriate phenology. House sparrows, *Passer domesticus*, expressed a rich array of vocalizations ranging from calls to multisyllabic songs and motifs of songs that varied under a regimen of different photoperiodic conditions that were simulated at different times of year. Control (SHAM) birds exhibited increases in song behavior when they were experimentally transferred from short days, simulating winter, to equinoctial and long days, simulating summer, and decreased vocalization when they were transferred back to short days. When maintained in long days for longer periods, the birds became reproductively photorefractory as measured by the yellowing of the birds' bills; however, song behavior persisted in the SHAM birds, suggesting a dissociation of reproduction from the song functions. Pinealectomized (PINX) birds expressed larger, more rapid increases in daily vocal rate and song repertoire size than did the SHAM birds during the long summer days. These increases gradually declined upon the extension of the long days and did not respond to the transfer to short days as was observed in the SHAM birds, suggesting that the pineal gland conveys photoperiodic information to the vocal control system, which in turn regulates song behavior.

Introduction

In temperate zone animals, annual cycles of many processes, including reproduction, metabolism, immune function, migration and song, are temporally controlled by an endogenous biological

timekeeping system or clock (Dawson et al., 2001, Goldman, 2001, Pittendrigh, 1993). This biological clock interprets environmental time—such as that marked by annual changes in photoperiod, temperature and other factors—and activates or terminates these processes at the appropriate time of the year. In seasonally breeding mammals, the pineal gland plays an important role in photoperiodic regulation of annual gonadal cycles (Hoffman and Reiter, 1965, Hoffman and Reiter, 1966, Reiter, 1973a, Reiter, 1973b). For example, pinealectomy (PINX) prevents gonadal regression in response to short winter-like photoperiods in both male and female hamsters (Hoffman and Reiter, 1966, Reiter, 1973a), and PINX hamsters remain reproductively competent in short-day environments (Reiter, 1973b). The daily duration of nocturnal melatonin released by the pineal gland reflects the photoperiod, such that melatonin duration is long during the long nights and short days of winter, whereas melatonin duration is short during the summer. This change in melatonin duration mediates the photoperiodic response of the hypothalamo-pituitary-gonadal (HPG) axis, which in turn regulates seasonal reproduction (Barrett et al., 2003, Dupre et al., 2008, Goldman, 2001, Lincoln, 2006) as well as other processes, such as pelage coloration and metabolism (Bartness et al., 1993).

The pineal gland is important for the generation and regulation of circadian rhythms in oscine passerine birds (Cassone, 1990, Gwinner and Hau, 2000). Although PINX house sparrows, *Passer domesticus*, entrain to light:dark (L:D) cycles, the surgery eliminates the expression of free-running circadian patterns of

locomotor behavior, song, body temperature and brain metabolism in house sparrows and several other species of passerine birds when they are maintained in constant environmental lighting such as constant darkness (D:D) or constant dim light (Binkley et al., 1971, Gaston and Menaker, 1968, Lu and Cassone, 1993a, Wang et al., 2012). Transplantation of a pineal gland into arrhythmic, PINX house sparrows confers both rhythmicity and time of day information (Zimmerman and Menaker, 1979). These effects are likely due to the circadian secretion of melatonin by the pineal gland, which, in contrast to galliform and columbiform birds, produces all of the circulating hormone in house sparrows (Janik et al., 1992). The pineal glands of all birds studied to date express circadian patterns of biosynthesis and secretion of melatonin in D:D that entrain to light:dark cycles (L:D) such that melatonin is released during the night (Brandstätter et al., 2000, Takahashi et al., 1980), and that rhythmic administration of the melatonin entrains locomotor rhythms of arrhythmic PINX birds (Cassone et al., 2008, Heigl and Gwinner, 1995, Lu and Cassone, 1993b, Wang et al., 2012).

In contrast to mammals, photoperiodic regulation of seasonal gonadal activity in birds is largely independent of the pineal melatonin system insofar as PINX has little effect on gonad size or activity in response to changes in photoperiod (Bentley, 2001, Dawson et al., 2001, Wilson, 1991). Nonetheless, the house sparrow pineal gland, as in seasonally reproducing mammals such as hamsters, expresses seasonal changes in melatonin duration in vivo and in vitro based upon the photoperiod in which birds were

raised (Brandstätter et al., 2000). Thus, whereas the avian pineal gland is important for circadian rhythms and whereas circadian rhythms are important for seasonal reproduction, the pineal gland is not directly involved in the regulation of the HPG axis (Bentley, 2001, Pant and Chandola-Saklani, 1992, Wilson, 1991).

As with the gonads (Dawson et al., 2001), the size and complexity of the song control system within the brains of male oscine passeriform birds change depending on the photoperiod (Ball et al., 2004, Brenowitz, 1997, Whitfield-Rucker and Cassone, 2000). The song control nucleus "HVC" (formerly "*h*igh *v*ocal *c*enter"), the robust nucleus of the archipallium (RA), Area X and the lateral magnocellular nucleus of the nidopallium (lMAN) are small during the short days of winter (when the bird is said to be "photosensitive") and grow 10–30% in volume as the photoperiod increases in the spring and summer (i.e., the bird becomes "photostimulated") (Brenowitz, 1997, Whitfield-Rucker and Cassone, 2000). If birds are experimentally maintained in long photoperiods for longer periods of time (10–20 weeks, depending on the species and photoperiod; Dawson et al., 2001), their gonads and song control systems become insensitive to the previously stimulatory effects of long photoperiod and spontaneously regress, a life history stage known as "photorefractory". Secretion of gonadal and neural steroids is important for changes in song control structures (Brenowitz, 1997, Tramontin et al., 2003), although they are not the only processes controlling song; castration has little effect on the photostimulatory effects of long

photoperiods on song control structures (Ball et al., 2004, Bernard et al., 1997, Whitfield-Rucker and Cassone, 2000).

One candidate molecule contributing to non-gonadal song control regulation is pineal melatonin. The distribution of melatonin binding sites and melatonin receptors in the avian brain suggests that the pineal hormone may regulate the song control system directly (Gahr and Kosar, 1996, Whitfield-Rucker and Cassone, 1996). In vitro binding of the melatonin agonist 2[^{125}I]-iodomelatonin (IMEL) and autoradiography in the male house sparrow, the zebra finch, *Taeniopygia guttata*, and the European starling, *Sturnus vulgaris*, reveal high-affinity IMEL binding in brain structures associated with the song control system, including Area X, HVC, lMAN and RA (Bentley and Ball, 2000, Gahr and Kosar, 1996, Whitfield-Rucker and Cassone, 1996). In house sparrows, at least, IMEL binding in the song control nuclei is not affected by castration (Whitfield-Rucker and Cassone, 1996). Although all three melatonin-receptor sub-types, Mel_{1A}, Mel_{1B}, and Mel_{1C}, are expressed in the song control system, Mel_{1B} is the predominant receptor sub-type in the song control system (Bentley et al., 2013, Jansen et al., 2005).

Melatonin affects the size and complexity of brain song control nuclei (Bentley et al., 1999, Cassone et al., 2008). Continuous melatonin administration to European starlings, which abolishes seasonal changes in melatonin duration, also decreases the amplitude of seasonal changes in the volume of the song control nuclei (Bentley et al., 1999). Rhythmic melatonin administration with long durations, as exemplified by winter conditions, entrains

locomotor rhythms of house sparrows maintained in constant light (L:L) and decreases the sizes of HVC and RA to winter-like volumes (Cassone et al., 2008).

To examine the pineal gland's role in seasonal changes of song behavior, we investigated the effect of PINX on song behavior under changing photoperiodic conditions in male house sparrows. Seasonal changes in song rates in wild populations have been observed in this species, with rate peaks occurring between late March and early August and nadirs around November (Hegner and Wingfield, 1986, Lowther and Cink, 2006). The present study investigates whether PINX affects photoperiodic changes in song behavior of singly housed male house sparrows. We hypothesize that the pineal gland, through the secretion of melatonin—which mirrors the photoperiod in duration—transduces such photoperiodic information to accurately synchronize the expression of avian vocal behavior to an appropriate time of year.

Section snippets

Animals and data acquisition

Adult male house sparrows, *P. domesticus* (N=22), were captured in August, 2012, around Lexington, KY, and were group housed with food (2:1 millet to chick starter) and water ad libitum in an aviary exposed to a natural photoperiod at the Ecological Research Facility, University of Kentucky in Lexington. In Winter 2012, birds at their photosensitive stage were transferred into individual cages in isolation cabinets with food and water ad libitum under L:D 6:18 (light at 40μW/cm2, lights on at 6…

The song repertoire of the house sparrow

As a “close-ended learner”, the house sparrow is commonly considered to have rather simple call and song repertoire, both of which are composed of single or a series of “cheep” or “chirrup” notes (Lowther and Cink, 2006). However, systematic analyses of vocalizations in male house sparrows reveal a larger and more complex repertoire in both call and song (Nivison, 1978), which this study corroborates. In this study, individual house sparrows were acoustically and visually isolated. We…

Discussion

In oscine passerine birds, the photoperiodic time-measurement system controlling seasonal aspects of primary reproductive function, such as gonadal regression and recrudescence, has in part been functionally separated from the photoperiodic control of complex secondary sexual characteristics, such as song (Bentley, 2001, Cassone et al., 2009). There is certainly a significant amount

of overlap, however. For example, song control nuclei express androgen and estrogen receptors (Ball et al., 2004…

Acknowledgments

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>
> …Apart from reproduction, several other functions exhibit well expressed seasonality, including metabolism and immunity. In avian species, migration and singing are also highly seasonal (Wang et al., 2014). All of these processes remain under the control of an endogenous biological clock, which is organized differently in mammals and birds (Bell-Pedersen et al., 2005)….

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> …There is extensive evidence that melatonin is also important in mammalian sleep: wake cycles. In seasonally breeding mammals, the hormone is critical for the transduction of photoperiodic information in the seasonal control of gonadal function [1–3], as well as seasonal control of birdsong and migration in passerine birds [4–6]. Melatonin is synthesized in pinealocytes in the pineal gland and in retinal photoreceptors [7]….

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> *Citation Excerpt :*
>
> …This suggests that the changes are indirect through gonadotropin-driven steroid release (see also Balthazart et al., 2010) but photoperiod also has a direct effect upon the size of the song nuclei (which is then amplified by steroids) (e.g. Robertson et al., 2014). The pathways for this direct effect may well operate through melatonin (Wang et al., 2014). If so they are again “indirect” and we are still looking for a true direct impact of day length on neural machinery.…

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