



Review

Transsynaptic trophic effects of steroid hormones in an avian model of adult brain plasticity



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ABSTRACT

The avian song control system provides an excellent model for studying transsynaptic trophic effects of steroid sex hormones. Seasonal changes in systemic testosterone (T) and its metabolites regulate plasticity of this system. Steroids interact with the neurotrophin brain-derived neurotrophic factor (BDNF) to influence cellular processes of plasticity in nucleus HVC of adult birds, including the addition of newborn neurons. This interaction may also occur transsynaptically; T increases the synthesis of BDNF in HVC, and BDNF protein is then released by HVC neurons on to postsynaptic cells in nucleus RA where it has trophic effects on activity and morphology. Androgen action on RA neurons increases their activity and this has a retrograde trophic effect on the addition of new neurons to HVC. The functional linkage of sex steroids to BDNF may be of adaptive value in regulating the trophic effects of the neurotrophin and coordinating circuit function in reproductively relevant contexts.

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1. Introduction

Seasonal changes of the environment that are critical to survival and reproduction have a pronounced effect on birds and essentially all other animals. It is therefore not surprising that seasonal plasticity of the adult brain has been observed in every vertebrate taxon (Tramontin and Brenowitz, 2000). The avian song control system provides the best model for studying the mechanisms and functional significance of seasonal plasticity in brain and behavior, with changes that are the most pronounced yet observed in any vertebrate model. Song is a learned stereotyped behavior that can be quantitatively analyzed, it is regulated by well-identified neural circuits, and testosterone (T) and its androgenic and estrogenic metabolites exert a strong influence on the morphology and physiology of these neural circuits.

Sex steroids released by the gonads or synthesized in the brain can serve various functions in the adult nervous system: (1) they activate neurons in sexually dimorphic brain regions to produce sex-typical behaviors; (2) hormones provide a means of restricting neural activity to appropriate environmental and physiological conditions, as seen in hormone-regulated growth of the song control system in birds early in the breeding season; and (3) secretion

of steroids by the gonads and transport to the brain can coordinate neural and behavioral activation with reproductive physiology. An example of this latter role is the vernal enhancement of song production by T in male birds to attract and stimulate mates at the time of year when the reproductive axis is optimized for breeding in both sexes (Ball et al., 2003). Steroids may act directly on neurons to have these effects. Neurons in limbic and other regions of the brain often have nuclear and/or membrane-bound receptors for different steroids. It has become clear recently that steroids may also have indirect actions on brain regions through transsynaptic mechanisms, even if neurons in the target regions lack steroid receptors. Transsynaptic trophic effects of steroids have been demonstrated most clearly in the context of seasonal plasticity of the adult avian song system, and that will be the focus of this review.

2. The avian song control system

Song is a learned behavior that is widely produced among the 4000 species of oscine songbirds and in many other avian taxa (Catchpole and Slater, 2008). Songs have well-defined acoustic structures that are characteristic of each species. In most species that breed in temperate and high latitude regions, song is produced largely or only by males. In many tropical species, however, females also sing and may join with males in producing complex vocal duets. There is extensive taxonomic diversity in the age when

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song is learned (Beecher and Brenowitz, 2005; Brenowitz and Beecher, 2005). In many species, referred to as age-limited learners, song learning is completed by the onset of sexual maturity late in the first year of life. Other species, known as open-ended learners, may continue to learn new songs as adults. Song plays important roles in avian reproduction (Catchpole and Slater, 2008). In many species, song is used to declare a territory from which other birds are aggressively excluded. Both males and females may use song in this context. In most songbird species males also use song to attract females. Females may select among potential mates on the basis of individual song characteristics. The male's song may directly stimulate reproductive behavior in females. In addition to these two main functions, song may be used in other behavioral contexts. For example, song may be important in mediating dominance behavior among members of a social group.

Song behavior is regulated by a discrete network of interconnected nuclei that arises in the pallium, projects to brainstem nuclei that control vocalization and respiration, and receives input from pallial auditory regions. (Some authors regard the avian pallium as homologous to mammalian cortex (Jarvis, 2009; Wang et al., 2010)). The song control system is organized into two functional pathways (Fig. 1, for review see, Zeigler and Marler, 2008). The main pathway for the motor production of song in adult birds includes projections from HVC to RA in the telencephalon, and from RA to nXIIIts in the medulla, which innervates the muscles of the sound-producing organ, the syrinx, and brainstem respiratory pre-motor nuclei. The anterior forebrain pathway (AFP) includes HVC, area X in the striatum, DLM in the thalamus, LMAN in the pallium, and RA; it is analogous to the mammalian basal ganglia-thalamocortical circuit (Luo et al., 2001). The AFP is essential for song learning, for the motor production of song in juveniles (Olviczky et al., 2005), and for adult song variability (reviewed in Brainard (2008)).

Steroid sex hormones affect song learning and production, and the juvenile development and adult plasticity of the song circuits (reviewed in Schlinger and Brenowitz (2009)). In those species examined thus far, nuclear androgen receptors are present in the song nuclei HVC, RA, LMAN, area X, ICo (intercollicular nucleus), and nXIIIts, as well as in the muscles of the syrinx. Classical nuclear estrogen receptors are found in HVC and ICo (Fig. 2, reviewed in Schlinger and Brenowitz (2009)).

3. Seasonality of breeding and song behavior in birds

Photoperiod is the primary environmental factor that influences activation of the avian reproductive system. In arctic, temperate, and subtropical birds, breeding is usually restricted to spring and early summer. Reproduction may also be seasonal in tropical species in which there are seasonal changes in environmental factors such as rainfall that influence breeding. Song behavior occurs most often or only in the breeding season in most species.

4. Seasonal plasticity in the brain

Seasonal changes in brain structure were first reported in the song system of domestic Canaries (*Serinus canarius*) by Nottebohm (1981). The song control system provides the most pronounced example of seasonal plasticity in an adult brain, and is the leading model for study of this process.

Seasonal changes in song behavior are accompanied by changes in the morphology of song nuclei in essentially every seasonally breeding songbird species that has been examined, including Rufous-collared Sparrows (*Zonotrichia capensis*) that breed seasonally in the foothills of the Andes on the equator (Moore et al., 2004). The volumes of HVC, RA, X, and nXIIIts increase by up to 200%

during the breeding season in both open-ended and closed-ended song learners. Cellular attributes of song regions also change (reviewed in Brenowitz (2008)). These seasonal changes can be observed *in vivo* using fMRI (De Groof et al., 2008). The spontaneous neurophysiological activity of RA neurons is greater in breeding White-crowned Sparrows (*Zonotrichia leucophrys*) and Song Sparrows (*Melospiza melodia*) than non-breeding birds (Meitzen et al., 2007a, 2007b, 2009).

Neuron number in HVC also changes seasonally. In wild-caught Song Sparrows, for example, neuron number in HVC increases from about 150,000 in the fall to 250,000 during the breeding season, a 67% increase (Smith et al., 1997). This change in neuron number results from seasonal patterns of cell death and ongoing neurogenesis. At the end of the breeding season, circulating T levels drop and there is an increase in the death of mature HVC neurons (Thompson, 2011; Thompson et al., 2007). There is a subsequent increase in the addition of new neurons to HVC in nonbreeding birds (Tramontin and Brenowitz, 1999; Alvarez-Buylla et al., 1990). The death of mature HVC neurons increases the addition of new neurons to HVC (Scharff et al., 2000; Thompson and Brenowitz, 2009), and does so by increasing neural stem cell proliferation in the adjacent ventricular zone (Larson et al., 2014).

5. Seasonal changes in song behavior

Seasonal changes in various aspects of song behavior accompany plasticity of the song circuits. In some species of birds, such as the Spotted Towhee (*Pipilo maculatus*) and Sedge Warbler (*Acrocephalus schoenobaenus*), song is produced only during the breeding season and is absent at other times of year. Other species, such as Song Sparrows, White-crowned Sparrows, and Canaries, sing throughout most of the year. Even in these year-round singers, however, song is produced at much higher rates during the breeding season.

Song structure also changes seasonally in year-round singers. Songs typically become more variable after the breeding season. The morphology of individual song syllables becomes less stereotyped in species including Canaries, Song Sparrows, and White-crowned Sparrows (Smith et al., 1997; Nottebohm et al., 1986; Brenowitz et al., 1998; Tramontin et al., 2000). Song Sparrows sing a greater number of variations of specific song types outside the breeding season (Smith et al., 1997). Songs also are shorter in non-breeding Song Sparrows, White-crowned Sparrows, and wild Island Canaries (Smith et al., 1997; Brenowitz et al., 1998; Leitner et al., 2001). The stereotypy of song duration and of the “fee” note of Black-capped Chickadees (*Poecile atricapillus*) is greater during the breeding season (Smulders et al., 2006). Stable song produced during the breeding season, however, does not change in structure from year to year in closed-ended learners like Song Sparrows and White-crowned Sparrows (Hough et al., 2000; Nordby et al., 2002).

6. Adaptive value of seasonal plasticity

What is the adaptive value of the extensive seasonal changes observed in the song circuits? Regrowing the song system each spring must impose an energetic cost. Is the cost of such yearly growth outweighed by some advantage that is gained? Other hormone sensitive regions of the avian brain, such as the hippocampus, do not undergo the seasonal regression and growth characteristic of the song system (Lee et al., 2001).

One hypothesis of the benefit of seasonal plasticity was presented by Nottebohm (1981) in the original study of this phenomenon in Canaries. Male Canaries develop new song patterns as adults, and do so in a seasonal manner. Nottebohm proposed that

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