

Testosterone and social context affect singing behavior but not song control region volumes in adult male songbirds in the fall

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Received 7 March 2007; received in revised form 19 November 2007; accepted 3 December 2007

Abstract

Testosterone (T) induces singing behavior and mediates changes in the sizes and neuroanatomical characteristics of brain regions controlling singing behavior (song control regions, SCRs) in songbirds. These effects may require the enzymatic conversion of T into androgenic and estrogenic metabolites by brain tissues and can be modulated by factors such as season and social context. Testosterone administration to adult male House Finches, *Carpodacus mexicanus*, in the spring increases the size of their SCRs. Here, we used males of this species to investigate effects of T and T metabolism on brain morphology and singing behavior in the fall. Birds received Silastic capsules containing androgens, estrogens, and/or inhibitors of androgenic action or estrogen synthesis to determine effects of these hormones on song rates and SCR volumes. We also manipulated the social environment by changing the number of birds in visual contact with each other. Testosterone treatment stimulated singing behavior in finches held in small, visually isolated groups and exposed to song playbacks. However, administration of T or T metabolites did not increase SCR sizes. The data suggest that photoperiodic condition and social context may modulate the effects of steroids on SCRs and singing behavior.

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Keywords: Neuroplasticity; Photoperiod; Steroid; Testosterone; Singing

1. Introduction

Gonadal steroid hormones act centrally to facilitate the expression of many behaviors, especially those associated with reproduction, such as singing in male songbirds (Ball et al., 2004; Harding, 2004). In many songbirds, seasonal patterns of singing behavior follow seasonal cycles of circulating gonadal steroids such that singing behavior increases in the spring, during the breeding season (Catchpole and Slater, 1995). Discrete regions in the songbird brain, collectively known as the song control regions (SCRs; Fig. 1) control the learning and expression of song (Nottebohm et al., 1976). These regions are sensitive to circulating steroid hormones and grow in response to elevated testosterone (T) levels, although in some species, effects of T on SCRs vary seasonally (Johnson and Bottjer, 1993; Bernard and Ball, 1997; Smith et al., 1997; Dloniak and Deviche, 2001).

In many seasonal breeders, photoperiod is the primary environmental factor that initiates development of the reproductive organs and drives an increase in circulating gonadal steroid hormone concentrations. During the late summer and early fall, many northern latitude, temperate zone songbirds undergo a period of photorefractoriness and lose sensitivity to the stimulatory effect of long days on their reproductive system (Hamner, 1968; Nichols et al., 1988). Photosensitivity in these species is gradually restored in response to short day exposure experienced during the fall and winter (Wilson and Donham, 1988; Dawson et al., 2001). Bernard and Ball (1997) demonstrated that T administration to adult male European Starlings, *Sturnus vulgaris*, stimulates the growth of one SCR, the HVC, in photosensitive but not photorefractory Starlings. However, in Dark-eyed Juncos, *Junco hyemalis*, T stimulates SCR growth regardless of photoperiodic condition (Dloniak and Deviche, 2001). Thus, when photorefractory, species may differ with respect to the sensitivity of their SCRs to T.

The sensitivity of the brain to T may change as a result of differences in steroid receptor densities or in the ability of the brain to convert T into active or inactive metabolites. The avian

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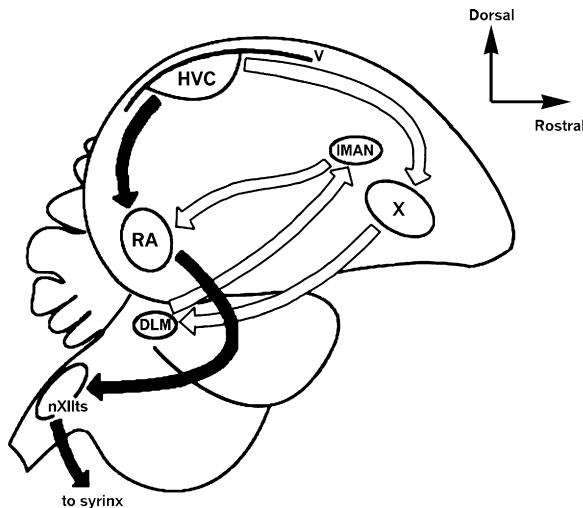


Fig. 1. Schematic drawing of the song control regions. The black arrows indicate the descending motor pathway and the open arrows indicate the anterior forebrain pathway. HVC: acronym used as common name; RA: Robust nucleus of the arcopallium; X: Area X; DLM: dorsolateral nucleus of the medial thalamus; IMAN: lateral magnocellular nucleus of anterior nidopallium; nXIIIts: the tracheosyringeal portion of the hypoglossal nucleus.

brain contains the enzyme aromatase that converts T into the estrogen 17β -estradiol (E_2 ; Schlinger, 1997; Soma et al., 1999b; Saldanha et al., 2000) and some SCRs contain both androgen and estrogen receptors (Balthazart et al., 1992; Gahr et al., 1993; Gahr and Metzdorf, 1997). In adult male White-crowned Sparrows, *Zonotrichia leucophrys gambelii*, the density and number of cells containing androgen receptors in the HVC decreases in the fall (Soma et al., 1999a). Furthermore, in this species held under spring-like conditions, administration of either T, the non-aromatizable androgen dihydrotestosterone (DHT), E_2 , or a combination of DHT and E_2 increased SCR volumes compared to controls (Tramontin et al., 2003). When the conversion of T into E_2 was inhibited, adult male Song Sparrows, *Melospiza melodia*, had decreased SCR volumes in the spring, but not in the fall (Soma et al., 2004). However, adult male Canaries, *Serinus canaria*, responded to T treatment by increasing singing behavior and HVC volume whereas treatment with either DHT or E_2 had no such effects (Sartor et al., 2005). Singing rates were reduced in Red-winged Blackbirds, *Agelaius phoeniceus*, exposed to androgens or estrogens alone and in Song Sparrows when the conversion of T into E_2 was inhibited (Harding et al., 1988; Soma et al., 2000a,b), indicating that the combined effects of T and E_2 contribute to stimulating singing behavior. Given these varied results, the influence of androgens and estrogens on singing behavior and SCR volumes of birds exposed to varying photoperiodic conditions deserves further scrutiny.

Social context can also affect singing behavior and SCR growth. For example, Tramontin et al. (1999) found that male White-crowned Sparrows housed with females sang more and had larger SCRs than isolated birds or birds housed with males. Furthermore, Boseret et al. (2006) found that T-treated male Canaries sang more often when they were housed with other males than with females. Interestingly, in this study, HVC volumes were larger in males housed with females than with males,

even though they sang less often. In free-living male Barn Swallows, *Hirundo rustica*, during the breeding season, there was no effect of social context (proximity of conspecific males) on song rate; however, social context affected other song characteristics such as song duration (Galeotti et al., 1997). Taken together, these observations suggest that the effects of the presence of a male or female on singing behavior differ across species. Therefore, the effectiveness of T treatment on singing and SCR volumes may also vary depending on the social context and species. Comparative studies taking into consideration differences in intraspecific social structures and responsiveness to photoperiod between songbird species may help to identify the mechanisms that contribute to regulating adult neuroplasticity.

We investigated the effects of T and T metabolism on SCR volumes and singing behavior in adult male House Finches, *Carpodacus mexicanus*, in the fall. House Finches belong to the same group of Cardueline finches as Canaries and Goldfinches. House Finches are often found in flocks, especially in the fall, and they sing year-round but most frequently in the spring, when they are breeding (Hill, 1993). Breeding in this species takes place in spring and early summer and the timing and extent of the breeding period are photoperiodically driven (Hamner, 1966, 1968). Two experiments tested the following hypotheses: (1) T treatment in the fall stimulates singing and increases SCR volumes. (2) Effects of T on SCRs and singing result from combined effects of androgens and estrogens. (3) Effects of T on SCRs and singing depend on the social context. Specifically, acoustic or visual contact with conspecific males influences the effectiveness of T to increase SCRs or singing.

2. Materials and methods

2.1. Animals

Between May and October 2000, 56 adult male House Finches and in August and September 2001, 42 adult male House Finches were captured from the local population in Tempe, AZ ($33^{\circ}25'N$; $111^{\circ}55'W$), using seed-baited Potter traps. Commercial finch chow and water were available *ad libitum*. The Arizona State University Institutional Animal Care and Use Committee approved all experimental protocols. Scientific collecting permits from the Arizona Game and Fish Department and the United States Fish and Wildlife Service were secured before birds were captured.

We studied males in the fall, when these birds have regressed testes and low plasma T (<0.22 ng/ml; Hamner, 1966, 1968; unpublished data). At the time of capture, birds were in breeding condition or were photorefractory. Free-living adult male House Finches maintain large testes and elevated plasma T during the spring and early summer, becoming photorefractory in late June or early July (Hamner, 1968; unpublished data). Photorefractory House Finches gradually regain photosensitivity beginning in late September and do not become fully photosensitive until December (Hamner, 1968). To induce and/or maintain photorefractoriness, birds were held in environmental chambers and exposed to artificial long days (16L:8D, LD) at $25^{\circ}C$ until the beginning of the experiments (see below). Some males used for

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