



The role of androgen receptors in regulating territorial aggression in male song sparrows

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ABSTRACT

This paper examines the role that androgen receptors (ARs) play in modulating aggressive behavior in male song sparrows, *Melospiza melodia morphna*. Song sparrows are seasonally breeding, territorial birds that maintain year-round territories with male–female pair bonds formed during the spring breeding season. Plasma testosterone levels peak as territories are established and mates acquired. In late summer, testosterone levels fall and remain basal during the non-breeding season. We examined the role of ARs in regulating territorial aggression in captive song sparrows under short- and long-day conditions as well as just prior to, and at the start of the breeding season in freely living birds using the nonsteroidal antiandrogen flutamide to block AR function. Birds were implanted with either empty or drug filled silastic implants for 18 to 42 days and then challenged with a novel male decoy to assess the individual birds level of male–male aggression. Freely living birds remained on their home territory and underwent a simulated territorial intrusion, whereas laboratory-held birds were assessed using a laboratory simulated territorial intrusion and remained in their home cage. Experimental treatment of male song sparrows decreased aggressive behavior during the pre-breeding life history substage (March–April) in freely living birds as well as in laboratory-held birds under long-day (16L:8D) conditions. During the early breeding substage (April–May) there was no measurable effect of flutamide treatment on aggressive behavior, nor was there a difference in behavior in the (8L:16D) laboratory birds. This demonstrates that ARs are an important component of the neuroendocrine control of aggressive behavior. Given that flutamide only affected aggression during the pre-breeding substage and in LD birds, the results suggest that AR dependent control of aggressive behavior changes as song sparrow life history states change.

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Introduction

There is a large body of evidence demonstrating that steroids, and in particular testosterone (T), are involved with the regulation of territorial aggression (Nelson, 1995; Wingfield et al., 1999). Within a reproductive context, aggression is activated by T (Simon et al., 1996; Wingfield et al., 1999) with circulating levels correlating with aggression only during socially unstable periods (i.e. the Challenge Hypothesis) (Wingfield et al., 1990). This relationship between T and aggression is present throughout the vertebrate classes (Nelson, 1995), but the mechanisms through which T exerts its effect are not fully understood. T can facilitate aggressive behavior primarily through either an androgenic or estrogenic pathway. The androgen receptor (AR) transcription factor is thought to be the principal target

for the androgenic pathway with T acting either directly or after being converted by the steroidogenic enzyme 5 α -reductase to the non-aromatizable androgen 5 α -dihydrotestosterone (DHT). T can also be converted to the primary estrogenic steroid 17 β -estradiol (E2) by the enzyme aromatase thus influencing aggression via either the α or β estrogen receptors (ER). There is also increasing evidence that there are non-genomic androgen and estrogen receptors in addition to the classical nuclear transcription factors (see Thomas et al., 2006) providing several other possible targets through which T can act.

The activation of the ER by E2 plays a central role in the activation of male aggressive behavior. In male mice, ER- α is the predominant ER target involved in the activation of aggressive behavior (Ogawa et al., 1998), whereas ER- β appears to be involved in inhibiting aggressive behavior during puberty and in young adult male mice (Nomura et al., 2002). In fact, based upon knockout studies, ER- α appears to be necessary for T induction of aggressive behavior (Ogawa et al., 1998). Although in birds there is no direct evidence for a role for either ER- α or - β , there is considerable evidence that E2 is necessary for males to exhibit territorial aggression (Soma et al., 2000a). This has been shown within reproductive (Schlinger and Callard, 1989; Soma et al., 2000a), as well as non-reproductive

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contexts (Soma et al., 2000b), but results do vary across species (Canoine and Gwinner, 2002).

There is strong evidence that in addition to the ER-mediated regulation of male aggressive behavior an androgen-mediated component is necessary for an animal to express a full suite of aggressive behaviors (reviewed in Simon, 2002). While there is evidence for a role for the primary androgens T and DHT in the regulation of aggressive behavior (e.g. Archawaranon and Wiley, 1988; Finney and Erpino, 1976; Ogawa et al., 1996), there is less known about AR mediated control. In fact, these studies suggest that the combination of estrogenic and androgenic steroids synergistically modulates aggressive behavior. However, the mechanisms through which androgens are acting are not well understood. The recent development of a complete AR knockout mouse has demonstrated that the absence of the AR protein results in reduced male territorial aggression (Sato et al., 2004). Thus, confirming that the AR is necessary for complete expression of aggressive behavior. However, this study also found that male aggression may be partially regulated through androgens acting via an AR-independent pathway distinct from the ER receptors (Sato et al., 2004). In non-mammalian vertebrates there is evidence of the importance of the AR mediated pathways using antiandrogens to prevent activation of the AR. Cyproterone acetate, a steroidal antiandrogen, decreased male territorial aggression in a lizard (*Anolis carolinensis*) (Deckel, 1996). In addition, flutamide, a nonsteroidal antiandrogen, was found to reduce aggressive behavior in the European robin (*Erithacus rubecula*) (Schwabl and Kriner, 1991) and red-winged blackbird (*Agelaius phoeniceus*) (Searcy and Wingfield, 1980).

In order to further our understanding of androgenic modulation of aggressive behavior we are using male song sparrows, *Melospiza melodia morphna*, as a model system. We examined the potential role of AR in regulating territorial aggression in both freely living and captive male song sparrows using flutamide to block AR function. The endocrine control of aggression in song sparrows has been extensively studied with a particular emphasis upon the seasonal and environmental control of aggression as well as the hormonal correlates to these behaviors (Soma et al., 2000a,b; Wingfield, 1994; Wingfield and Hahn, 1994). These birds defend multi-purpose breeding and feeding territories year-round and possess a well-defined set of behaviors consisting of combinations of visual displays and vocalizations that are involved with territorial defense against conspecific intruders (Nice, 1943; Wingfield, 1985; Wingfield and Monk, 1992). These behaviors can be readily measured in freely living birds using a standardized simulated territorial intrusion (STI) (Wingfield, 1985) as well as in captive birds held in controlled environments using a laboratory simulated territorial intrusion (LSTI) (Sperry et al., 2003). Studying both freely living and captive song sparrows allows us to examine birds under conditions where the myriad of social and environmental cues are all present as well as look at the birds' behaviors on a finer scale in the laboratory.

Within this paper we examine the role that ARs play in the control of aggression under both natural and laboratory conditions. Freely living birds were studied in the early part of the breeding season in order to focus on the time period when the male birds transition from their winter non-breeding life history stage to their spring breeding life history stage. During their non-breeding state, male song sparrows have regressed gonads and low to non-detectable circulating plasma T levels. As the birds move from this life history stage into the breeding life history stage, their levels of T increase as they establish territories and actively work to acquire and then defend mates and territories (Wingfield, 1985; Wingfield and Monk, 1992). Due to the rapid changes in levels of circulating T as the birds move between life history stages, we predicted that during these time periods the male song sparrows would be most sensitive to treatment with flutamide. For the purposes of this paper the term pre-breeding refers to the time period when male song sparrows are present on

their breeding territories, actively acquiring mates and possibly involved in pair bonding with potential mates but not yet ready to breed. Breeding refers to the time period early in the spring when the male birds have first begun to actively breed. Both are parts of the breeding life history stage with the pre- and early breeding time periods representing different substages. Note that song sparrows in the Pacific Northwest raise multiple broods and will breed throughout the late spring and summer. The laboratory studies examined both winter, non-breeding, aggression that is equivalent to short-day (SD) laboratory conditions and spring, breeding, aggression that is equivalent to long-day (LD) conditions. LD birds were also used to determine whether flutamide treatment had any unexpected behavioral or physiological side effects. In both cases, freely living song sparrows actively defend territories allowing us to address the question of whether ARs play a role in modulating breeding and non-breeding aggression.

Methods

Drugs

Flutamide (α -trifluoro-2-methyl-4'-nitro-*m*-propionotoluidide) was purchased from Sigma-Aldrich Co (product F9397). This drug was administered using silastic implants placed subcutaneously on the flanks of each song sparrow.

Field behavioral studies

The field studies were conducted in Western Washington State, USA between March 9 and April 19, 2001 and between April 20 and May 24, 2000. These time periods represent the song sparrows pre-breeding and early breeding life history substages, respectively (Wingfield and Hahn, 1994). Male song sparrows were caught using mist nets combined with conspecific playback. After capture, birds were immediately removed from the net and a blood sample was taken from the alar wing vein for determination of blood androgen levels. Measurements were taken for wing and tarsus length, mass and the length and width of the cloacal protuberance (CP). From the length and width measurements, a volume was calculated using the formula for a cylinder. In addition, abdominal and furcular fat was visually assessed using a standard five-point scale (see Wingfield and Farner, 1978). Birds were banded with fish and wildlife aluminum bands and given a unique set of color bands. In addition to body morphometrics, time to capture was determined. Time to capture is the amount of time elapsed between initiating song playback and the bird flying into the mist-net. After body morphometrics were recorded, each bird received three of either control (empty) or flutamide filled silastic implants. Silastic implants were 12 mm in length (1.47 mm i.d. and 1.96 mm o.d.) and sealed on both ends with 1 mm of clear silicone rubber sealant. Each implant was inserted through a small incision in the skin and sealed with nexaband liquid topical tissue adhesive (Abbott Laboratories, Chicago, IL, USA) followed by New-skin liquid bandage (Medtech, Chicago, IL, USA). Two implants were placed onto the left flank and the third implant was placed onto the right flank.

Territorial aggression for each male was quantified using a simulated territorial intrusion (STI) (Wingfield, 1994) 18 days after the birds received silastic implants. STIs were conducted using a caged conspecific decoy placed near the center of the territory combined with conspecific playback. Care was taken to place the decoy away from the location where the focal bird was previously captured. Two different playback tapes were used and each contained songs from a single male repeated every 10 s with a 1 min silence after every 2 min of song. The song type changed after each 2 min of song. The STI consisted of 10 min of observation of the focal bird with the decoy present and playback on. The persistence portion of the STI included 10 min of observation to measure the persistence of the response with

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