

Behavioral evidence for sex steroids hypersensitivity in castrated male canaries

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ABSTRACT

In seasonally breeding songbirds such as canaries, singing behavior is predominantly under the control of testosterone and its metabolites. Short daylengths in the fall that break photorefractoriness are followed by increasing daylengths in spring that activate singing via both photoperiodic and hormonal mechanisms. However, we observed in a group of castrated male Fife fancy canaries maintained for a long duration under a short day photoperiod a large proportion of subjects that sang at high rates. This singing rate was not correlated with variation in the low circulating concentrations of testosterone. Treatment of these actively singing castrated male canaries with a combination of an aromatase inhibitor (ATD) and an androgen receptor blocker (flutamide) only marginally decreased this singing activity as compared to control untreated birds and did not affect various measures of song quality. The volumes of HVC and of the medial preoptic nucleus (POM) were also unaffected by these treatments but were relatively large and similar to volumes in testosterone-treated males. In contrast, peripheral androgen-sensitive structures such as the cloacal protuberance and syrinx mass were small, similar to what is observed in castrates. Together these data suggest that after a long-term steroid deprivation singing behavior can be activated by very low concentrations of testosterone. Singing normally depends on the activation by testosterone and its metabolites of multiple downstream neurochemical systems such as catecholamines, nonapeptides or opioids. These transmitter systems might become hypersensitive to steroid action after long term castration as they probably are at the end of winter during the annual cycle in seasonally breeding temperate zone species.

1. Introduction

Sex steroid hormones play a critical role in both the development during ontogeny and in seasonal changes of singing behavior in songbird species such as canaries (Ball et al., 2002; Schlinger and Brenowitz, 2002). They exert these effects mostly by binding to androgen and estrogen receptors that are expressed within the network of brain nuclei dedicated to the control of singing behavior (Bernard et al., 1999; Metzdorf et al., 1999), such as in the nucleus HVC (used as a proper name), as well as in sites involved in activating singing motivation, such as the medial preoptic nucleus (Alward et al., 2013; Alward et al., 2016b; Ball et al., 2004; Ball et al., 2002; Bernard et al., 1999; Ritters and Ball, 1999; Ritters et al., 2000). Accordingly, many species exhibit marked increases in singing in the spring in correlation with gonadal growth and egg laying by the female but there is significant variation among species (Catchpole and Slater, 2008).

Implanting exogenous testosterone increases while castration decreases the frequency and duration of singing in males and females of many songbird species (Arnold, 1975; Madison et al., 2015; Nottebohm, 1980; Pröve, 1974). These effects of testosterone on multiple aspects of song are in many cases mediated by a synergistic action of its androgenic and estrogenic metabolites (reviewed in (Ball et al., 2003; Ball et al., 2002; Schlinger and Brenowitz, 2009)).

In many species, such as canaries, it is clear that testosterone alone can increase HVC volume even under short-day photoperiods to values typical of breeding conditions (Madison et al., 2015; Rouse Jr. et al., 2015; Sartor et al., 2005). Many laboratory studies assess singing and brain plasticity in the song system under conditions of long day lengths and high concentrations of testosterone (e.g., (Meitzen et al., 2007; Schlinger and Brenowitz, 2009; Small et al., 2015)). It is important to note that the ability to initiate breeding in photoperiodic species actually occurs in the fall when birds experience short days and break

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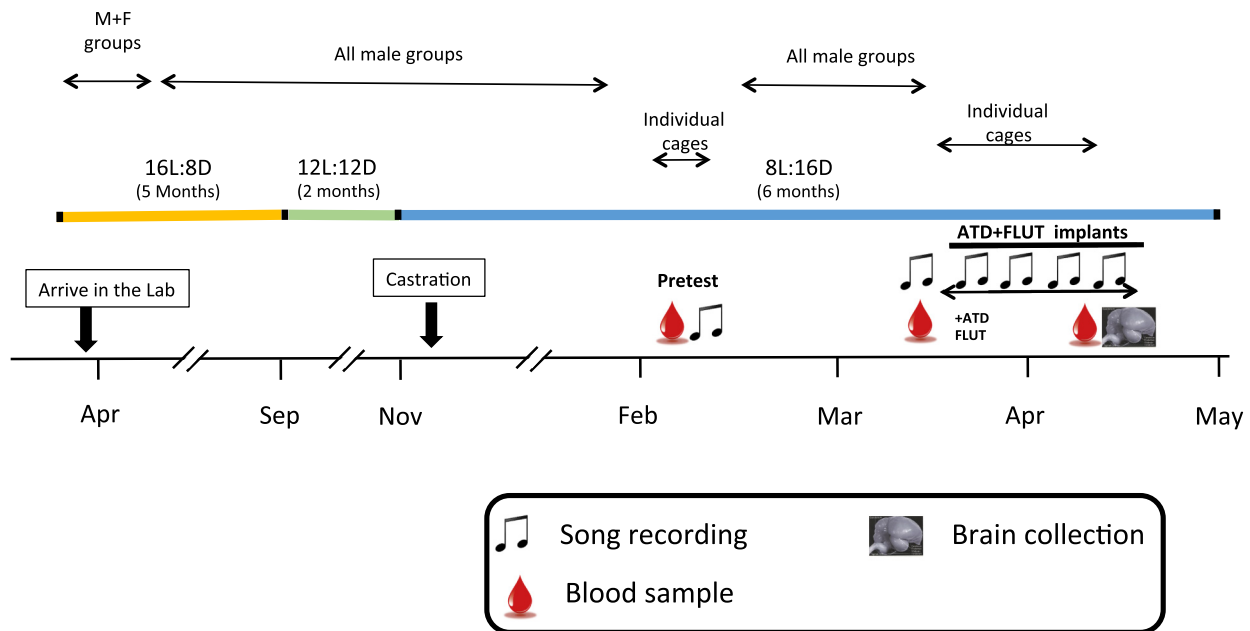


Fig. 1. Schematic representation of the endocrine and photoperiodic background of the males used in this experiment. The duration of each experimental phase is indicated by the months on the time line and further described in detail in the text but the durations are not strictly proportional to their length in the figure to allow representation of the experimental phase.

photorefractoriness (Dawson et al., 2001; Dawson and Sharp, 2007). Breaking photorefractoriness is associated with the activation of the hypothalamo-pituitary-gonadal (HPG) axis as measured by an upregulation of the message and protein for gonadotropin-releasing hormone (GnRH-I; (Dawson and Sharp, 2007; Stevenson et al., 2013)). Non-photoperiodic cues such as weather, food and social interactions can stimulate the HPG in these photosensitive birds on short days to engage in reproduction to varying degrees (Dawson and Sharp, 2007; Hahn et al., 1997). Field studies in canaries have revealed that populations can breed in December in some years well before the increase in photoperiod has occurred if other cues such as increases in rainfall are present (Leitner et al., 2003). Studies in the field on other species have revealed that song nuclei such as HVC can grow well before testosterone reaches maximal concentrations and is still quite low. This phenomenon has been described in blue tits (Caro et al., 2005b) and song sparrows (Tramontin et al., 2001). HVC volume also increases in response to long-day photoperiods in castrated male American tree sparrows (*Spizella arborea*) (Bernard et al., 1997).

Despite the important role of testosterone in song activation, some songbird species continue to sing during the non-breeding season when testosterone plasma concentrations are very low. For example, European starlings (*Sturnus vulgaris*) sing throughout the year, but their songs are shorter in autumn than in spring (Eens, 1997; Eens et al., 1994; Ritters et al., 2000). Field studies of wild canaries reveal singing in the non-breeding and breeding season although there are differences in song quality (Leitner et al., 2001). Male song sparrows (*Melospiza melodia*) also continue to sing in autumn but with greater variability compared to spring (Baker et al., 1984; Smith et al., 1997a). Although circulating testosterone concentrations are very low and castration does not decrease song in autumn, singing behavior in this species is still under the control of sex steroid hormones as evidenced by the fact that autumn song rate is decreased by a combined treatment with an aromatase inhibitor and an androgen receptor blocker or with an aromatase inhibitor alone (Soma et al., 1999; Soma et al., 2000). Multiple lines of evidence indicate that dehydroepiandrosterone (DHEA), an androgen produced by the adrenals, which in contrast to testosterone and estradiol is elevated during the non-breeding season in song sparrows (Soma and Wingfield, 2001), is activating autumn singing, likely

via its neural metabolism to androgens and estrogens, but possibly via other mechanisms too (for review see (Soma et al., 2015)).

In laboratory conditions, castrated male canaries do not sing or sing at very low rates following castration (Alward et al., 2013; Alward et al., 2016b; Balthazart et al., 2008). We report here that in castrated male canaries maintained on short-day photoperiod for an extended length of time, approximately two thirds of the subjects started singing at very high rates despite having low circulating testosterone concentrations. Treating subjects with the aromatase inhibitor androstatrienedione (ATD) combined with the anti-androgen flutamide barely affected the behavior and had minimal or no effect on steroid-dependent morphological and neuroanatomical measures. Together these data suggest that after extensive deprivation of sex steroid hormones, singing behavior can be activated by low concentrations of testosterone or its metabolites suggesting that mechanisms mediating behavioral activation have become hypersensitive to extremely low concentrations of sex steroids. In addition the present study identified major discrepancies between circulating concentrations of testosterone as measured by enzyme immunoassay (EIA) and by gas chromatography combined with mass spectrometry (GC/MS), in particular in birds treated with ATD and flutamide. These important methodological issues are also discussed.

2. Materials and methods

2.1. Subjects

Twenty-six male canaries of the Fife fancy breed were obtained from a colony maintained at the University of Antwerp, Belgium. They were born and had gone through a full breeding cycle in this colony where they were maintained on natural daylight during the months preceding their arrival in our laboratory at the University of Liege, Belgium, in late March. All experimental procedures complied with Belgian laws concerning the Protection and Welfare of Animals and the Protection of Experimental Animals, and experimental protocols were approved by the Ethics Committee for the Use of Animals at the University of Liege (Protocol number 1739). In all housing situations food, water, baths, cuttlebone and grit were available ad libitum.

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