



Antagonism of syringeal androgen receptors reduces the quality of female-preferred male song in canaries



Beau A. Alward^{a, b, *}, Farrah N. Madison^{a, b}, William T. Gravley^a, Gregory F. Ball^{a, b}

^a Department of Psychological and Brain Sciences, Johns Hopkins University, Baltimore, MD, U.S.A.

^b Department of Psychology, University of Maryland, College Park, College Park, MD, U.S.A.

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Adaptive performance of social behaviours requires the temporally precise activation of the relevant neural circuits based on the state of the environment. The actions of steroid hormones such as testosterone and its metabolites are critical in this activation for many social behaviours, especially those related to reproduction. Androgens, specifically androgenic action in the periphery, have been strongly implicated in regulating features of social behaviours that are considered to be especially important in mate attraction. Nevertheless, we currently have a relatively poor understanding of the different roles of steroid hormones in the regulation of social behaviour and its relevance to sexually selected traits. Here, we treat male canaries, *Serinus canaria*, with bicalutamide, an androgen receptor antagonist that does not cross the blood–brain barrier. Thus, we isolated androgen action to the periphery in order to target the syrinx, the avian vocal production organ. Bicalutamide treatment reduced song complexity but not song acoustic stereotypy. Bicalutamide-treated birds also showed reduced performance of ‘special trills’ and disrupted special syllable morphology. The performance and complexity of special trills in particular are able to stimulate copulation solicitation displays in female canaries to a substantially higher degree than any other component of canary song. These results highlight the nonredundant actions of steroid hormones in coordinating features of a complex behavioural pattern into an adaptive response, and suggest that androgen receptor expression in the relevant peripheral organs acts as a substrate on which sexual selection acts to amplify features of reproductive behaviours directly related to mate attraction.

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One important dimension of the optimal performance of social behaviours is that they are produced at the right time in relation to a changing environment. Steroid hormones are widely considered to play a key role in orchestrating the peripheral and central neural circuits involved in optimal behavioural output (Adkins-Regan, 2009; Pfaff, Schwartz-Giblin, McCarthy, & Kow, 1994; Wingfield, Hegner, Dufty, & Ball, 1990). Nevertheless, it is unclear how steroid hormones integrate across different target sites to regulate the different traits involved in the adaptive performance of a single complex behaviour. The hormonal control of birdsong is an excellent system in which to investigate these mechanisms.

Songbirds (oscines, members of the suborder Passeri) possess an interconnected network of telencephalic nuclei called the song control system (SCS) that orchestrates song learning and production (Brainard & Doupe, 2013; Fee & Scharff, 2010; Nottebohm, Stokes, & Leonard, 1976; Vu, Mazurek, & Kuo, 1994). HVC and the

robust nucleus of the arcopallium (RA) regulate the production of song while Area X and the lateral magnocellular nucleus of the anterior nidopallium (LMAN) are involved in the auditory feedback used to learn and maintain adult song. RA in turn projects to the tracheosyringeal portion of the nucleus XIIth cranial nerve (nXIIts, also called the hypoglossal nucleus) located in the hindbrain. Neurons in nXIIts project directly to the syrinx, the avian vocal organ. RA also projects to areas involved in respiration in the hindbrain such as nucleus retroambigualis (RAM) and the ventral respiratory group (VRG) (Nottebohm, Paton, & Kelley, 1982; Wild, 2008). The motor programme in the brain regions of the SCS thus converges onto syringeal and respiratory muscles to generate song. Indeed, the distinct acoustic structure of birdsong is due to the actions of specialized muscles that modulate airflow through the syrinx (Wild, 2008). Specifically, connective tissue controlled by the syringeal muscles are adducted into the syringeal lumen to gate airflow and vibrate during song (Larsen & Goller, 1999; Suthers, 2004). Other muscle groups and body parts, such as the jaw and beak, as well as the posture of the bird also may all play a role in modulating the acoustic structure of birdsong (Wild, 2008).

* Correspondence and present address: B. A. Alward, Department of Biology, Stanford University, Stanford, CA 94305, U.S.A.

E-mail address: balward@stanford.edu (B. A. Alward).

The syrinx is located in the chest inside of an airsac, which is connected to other airsacs and the lungs (Suthers, 2004). The syrinx surrounds the area where the two bronchi meet at the trachea. The songbird syrinx is considered to be the most complex among birds. Indeed, six pairs of muscles control the songbird syrinx, while two pairs control the dove syrinx (Suthers, 2004). It is generally believed that the large number of muscles controlling the syrinx allows for more configurations of the syrinx and thus gives rise to complex birdsong. The dorsal and ventral syringeal muscles are involved in controlling the two most important aspects of birdsong, its acoustic frequency and timing, respectively (Suthers, 2004; Vicario, 1991a, 1991b). Contraction of the dorsal muscles adducts the labia into the syringeal lumen, forming a slit that leads to oscillations as air flows across (Goller & Suthers, 1995; Larsen & Goller, 1999). Stronger contractions of these muscles that eventually close this slit on a particular side of the syrinx stop airflow and prevent labial oscillation, and thus sound produced through that particular side. The ventral syringeal muscles are involved in regulating the acoustic frequency of song by varying the tension of the oscillating labia (Goller & Suthers 1995, 1996).

Many studies have assessed how hormones such as testosterone affect song in songbirds. Castration drastically reduces song output based on studies in several species (Alvarez-Borda & Nottebohm, 2002; Alward, Balthazart, & Ball, 2013, 2016; Arnold, 1975; Harding, Walters, Collado, & Sheridan, 1988; Sartor, Balthazart, & Ball, 2005). There is evidence that testosterone does more than just affect song rate. Song during the breeding season, when circulating levels of testosterone are high in temperate-zone species, including white-crowned sparrows, *Zonotrichia leucophrys*, and canaries, can be more stereotyped and of longer duration as compared to the nonbreeding season, when circulating levels of testosterone are low (Smith, Brenowitz, Beecher, & Wingfield, 1997; Voigt & Leitner, 2008). Moreover, birds like canaries include more vocalization types called 'special trills' during the breeding season (Voigt & Leitner, 2008), which are referred to as such given their unique ability to elicit copulation solicitation displays in females to a higher degree than any other component of canary song. There are multiple potential sites of steroid hormone action in the SCS that could be involved in the regulation of song. Androgen receptors (ARs) are expressed in the HVC, RA, LMAN and throughout the hypothalamus and midbrain while oestrogen receptors (ERs) are expressed in the HVC of some species as well as in the hypothalamus (Ball, Ritters, & Balthazart, 2002; Bernard, Bentley, Balthazart, Turek, & Ball, 1999; Metzendorf, Gahr, & Fusani, 1999). ARs are also expressed in hindbrain nuclei involved in song such as nXIIIs and RAM while ERs are absent from these regions (Gahr & Wild, 1997; Metzendorf et al., 1999). ARs, but not ERs, are expressed in the muscles of the syrinx (Lieberburg & Nottebohm, 1979; Veney & Wade, 2004). Specifically, ARs are expressed in both the dorsal and ventral muscles of the syrinx as well as the labia (Veney & Wade, 2004). In songbirds, very low levels of AR expression have been detected in the other peripheral regions that have been assessed, such as the leg and wing muscles (Feng, Katz, Day, Barske, & Schlinger, 2010). There are currently no studies we are aware of that have investigated AR expression in muscles directly related to respiration.

By and large, it appears that testosterone and its metabolites act at multiple regions of the SCS, hypothalamus and hindbrain as well as the muscles of the syrinx to coordinate the specific features of song into a functional response (Alward et al., 2013; Meitzen, Moore, Lent, Brenowitz, & Perkel, 2007). This is consistent with views set forth by others (Arnold, 1981; Beyer & Feder, 1987; Lee & Pfaff, 2008; Pfaff, Kow, Loose, & Flanagan-Cato, 2008), who argue that steroid hormones must act at multiple loci to regulate the suite of traits that make up a single behaviour. For instance, recent work has shown that testosterone in the medial preoptic nucleus (POM)

regulates the motivation to sing but not song quality, while T in the HVC does not regulate the motivation to sing but is required to enhance song quality (Alward et al., 2013, 2016; Meitzen et al., 2007).

Females tend to prefer song that is complex and/or physiologically demanding to produce as it is an honest indicator of male quality (Byers, Hebets, & Podos, 2010; Gil & Gahr, 2002; Kubli & MacDougall-Shackleton, 2014; MacDougall-Shackleton, 1997; Pfaff, Zanette, MacDougall-Shackleton, & MacDougall-Shackleton, 2007; Sakata & Vehrencamp, 2012). Canaries have been studied extensively in this regard. Female canaries perform more nest building and lay more eggs when exposed to more complex songs (Kroodsma, 1976). Male canaries also produce a special type of syllable in their trills, which are notes sung successively in a rapid fashion (Catchpole & Slater, 2003; Podos, 1997; Fig. 1). These 'special syllables' have a two-note structure and are sung at very fast repetition rates (on average 16 or more syllables/s), traits that make them physiologically difficult to produce (Suthers, Vallet, & Kreutzer, 2012; Suthers, Vallet, Tanvez, & Kreutzer, 2004; Vallet & Kreutzer, 1995; Vallet, Beme, & Kreutzer, 1998) and thus more attractive to females (Byers et al., 2010; Podos, Huber, & Taft, 2004; Sakata & Vehrencamp, 2012). As mentioned above, special syllables (called sexy syllables by some) are labelled as such given their unique ability to elicit copulation solicitation displays from females (Vallet & Kreutzer, 1995; Vallet et al., 1998). Female canaries produce eggs with higher concentrations of androgens when exposed to male song containing special syllables compared to male song without special syllables (Gil, Lebouche, Lacroix, Cue, & Kreutzer, 2004), which may lead to larger offspring expressing a dominant phenotype. Females prefer trills that are sung at faster repetition rates (Byers et al., 2010; Drăgănoiu, Nagle, & Kreutzer, 2002; Sakata & Vehrencamp, 2012). They also prefer special trills produced at a lower pitch (Pasteau, Nagle, & Kreutzer, 2007).

One study has shown that the conversion of testosterone to oestrogen is required for the 'production' of special trills by canaries, but this conversion is not involved in modulating the 'features' of these trills (e.g. syllable repetition rate) that are most relevant to females (Rybak & Gahr, 2004). As mentioned above, ARs, but not ERs, are expressed in the muscles of the adult songbird syrinx (Lieberburg & Nottebohm, 1979; Veney & Wade, 2004), making the syrinx a plausible target of testosterone action in the control of song. However, the question of the effects of testosterone action specifically at the level of the syrinx in the regulation of avian vocalizations has been addressed only recently. In a suboscine, the golden-collared manakin, *Manacus vitellinus*, males treated with bicalutamide (BICAL), an AR blocker that does not cross the blood–brain barrier (Furr & Tucker, 1996), caused changes in the temporal and frequency characteristics of their 'chee-poo' call (Fuxjager, Heston, & Schlinger, 2014), a vocalization produced by the male as part of a complex suite of behaviours involved in courting a female (Fuxjager, Longpre, Chew, Fusani, & Schlinger, 2013). Specifically, BICAL caused an increase in the duration of the chee note and an increase in the fundamental frequency of the poo note. In oscine songbirds, there is no direct evidence for the role of testosterone at the syrinx in the regulation of song, but the study by Fuxjager et al. (2014) suggests that ARs at the syrinx could participate in regulating features of song related to attracting a mate.

In the current study, we treated male canaries with BICAL to test the role of androgen action at the syrinx in the regulation of song. BICAL is an extremely effective and fast-acting AR antagonist (Furr & Tucker, 1996). Indeed, Fuxjager et al. (2013, 2014) observed effects on display behaviours in male golden-collared manakins 1 day following BICAL treatment. As BICAL does not cross the blood–brain barrier, and the syrinx is the most behaviourally relevant AR-dense organ in the periphery in regards to birdsong production,

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