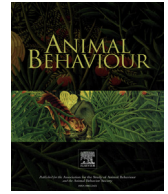




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Testosterone regulates birdsong in an anatomically specific manner

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The functions of birdsong include attracting a mate and repelling competitors. It is therefore not surprising that, in males in the temperate zone especially, birdsong is often produced in the context of reproduction. Testosterone of gonadal origin increases during the reproductive phase of the annual cycle and can significantly influence song production as well as song development via effects on song crystallization (testosterone secretion at the time of sexual maturity is essential for full crystallization to occur). In males, testosterone of gonadal origin can exert its effects in the brain on song and other reproductive behaviour via its oestrogenic and androgenic metabolites. The widespread distribution of nuclear androgen receptors in the song system and the occurrence of oestrogen receptors in one key forebrain nucleus in certain species as well as the presence of both receptor types in the diencephalon and the midbrain raises questions as to where and how testosterone is exerting its myriad effects on song. By selectively implanting testosterone into specific brain regions of castrated male canaries, *Serinus canaria*, we have identified the medial preoptic area as a critical site for the induction of a generalized increase in motivation that includes the motivation to sing. Testosterone action in the forebrain song nucleus HVC in contrast increases song stereotypy. Canaries receiving testosterone in the preoptic area and HVC sing stereotypic songs but at a much lower amplitude, indicating that testosterone's effects on amplitude are regulated elsewhere in the brain or the periphery. The lateral part of the magnocellular nucleus anterior nidopallium (LMAN) is a song nucleus that expresses a high density of androgen receptors and plays a role as a song variability generator during song learning. When adult female canaries are treated with testosterone, their song becomes more complex. Lesions to LMAN attenuate these effects on adult behavioural change, suggesting that testosterone may act in LMAN during song ontogeny to modulate changes associated with song crystallization. These anatomically specific effects illustrate how a single hormone can coordinate changes in many aspects of a complex behaviour to facilitate successful reproduction.

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STEROID HORMONES AND THE REGULATION OF BIRDSONG

Communication behaviour occurs in a particular social and environmental context (Hauser, 1996; Wiley, 2015). It is often desirable from a fitness perspective for individuals to relay information to conspecifics about a wide variety of stimuli in the environment such as the availability of food, the presence of predators or one's motivation to mate (Hauser, 1996; Owings & Morton, 1998). The appropriate signals must therefore be coordinated with the occurrence of a variety of other exogenous and

endogenous stimuli to be successful in promoting individual fitness. Communication in the context of reproduction is an excellent example of how signalling between males and females in sexually reproducing species must often be coordinated with a propitious time of the year to breed. This communication must also take into account the physiological condition of the signaller and the receiver for the signals to be produced at the best time to maximize fitness (Searcy & Andersson, 1986). The endocrine system plays a key role in coordinating suites of traits so that they occur in an organized and adaptive manner (Lee & Pfaff, 2008). Steroid hormones in particular can circulate in the blood and act as transcription factors at many different sites, including the brain, to coordinate complex suites of morphological, physiological and behavioural traits into an organized adaptive response to a particular adaptive goal (McEwen, Gray, & Nasca, 2015).

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Birdsong is often produced in the context of reproduction and functions to attract males and/or to repel competitors for access to mates (Catchpole & Slater, 2008; Collins, 2004; Kroodsma & Byers, 1991). Although the vocalization designated as the 'song' of a particular species is often the most complex, it is not the case in all species, as song is defined based on function rather than spectral complexity (Catchpole & Slater, 2008). Usually the term 'birdsong' is reserved for members of the songbird order, Passeriformes. This is the largest of all avian orders and consists of close to 50% of the roughly 10 000 living species of birds. This order can be broadly divided into two suborders, one of which (Passeres or oscines) contains most of the living passeriform species. They were first defined by the complexity of their vocal production organs, the syrinx, but can now also be distinguished by the fact that song produced by members of this suborder is clearly learned during development. Song learning is based on both various innate predispositions to develop song in a particular way and on the imitation of song produced by adult conspecifics. The fact that song is learned in a manner akin to human language has made the study of song development an area of intense interest among those studying cognitive development (Brainard & Doupe, 2013).

It was realized very early in studies of birdsong that in temperate zone species, song is produced at a high rate in a male-biased fashion in association with the onset of the breeding season (e.g. Catchpole & Slater, 2008; White, 1789). This observation led to the hypothesis that song was regulated by gonadal steroid

hormones. Experimental studies involving castration and testosterone replacement implemented in zebra finches, *Taeniopygia guttata*, did indeed confirm that testosterone could greatly enhance the probability of males producing song (Arnold, 1975; Pröve, 1974). Extensive subsequent experiments as well as studies correlating concentrations of testosterone in the blood with behaviour confirmed that one can discern a relationship between testosterone action and the occurrence of male-typical birdsong in wild and domesticated species (see reviews in: Harding, 2008; Schlinger & Brenowitz, 2009). Note, however, that the relationship between circulating concentrations of steroids in the blood and the occurrence of singing behaviour is not always linear (e.g. Schwabl et al., 2015). Behaviours such as song are often no longer enhanced after an optimal threshold concentration of a steroid hormone is reached (e.g. the breeding baseline described in Wingfield, Hegner, Dufty, & Ball, 1990), and in these cases one would not expect to observe correlations between behavioural rates and hormone concentrations (Ball & Balthazart, 2008).

THE SONG CONTROL SYSTEM AND THE EXPRESSION OF ANDROGEN AND OESTROGEN RECEPTORS

When studies on hormonal regulation of song were first conducted, it was discovered that song behaviour is mediated by a neural system of discrete brain nuclei (Nottebohm, Stokes, & Leonard, 1976; for a review of these initial studies, see;

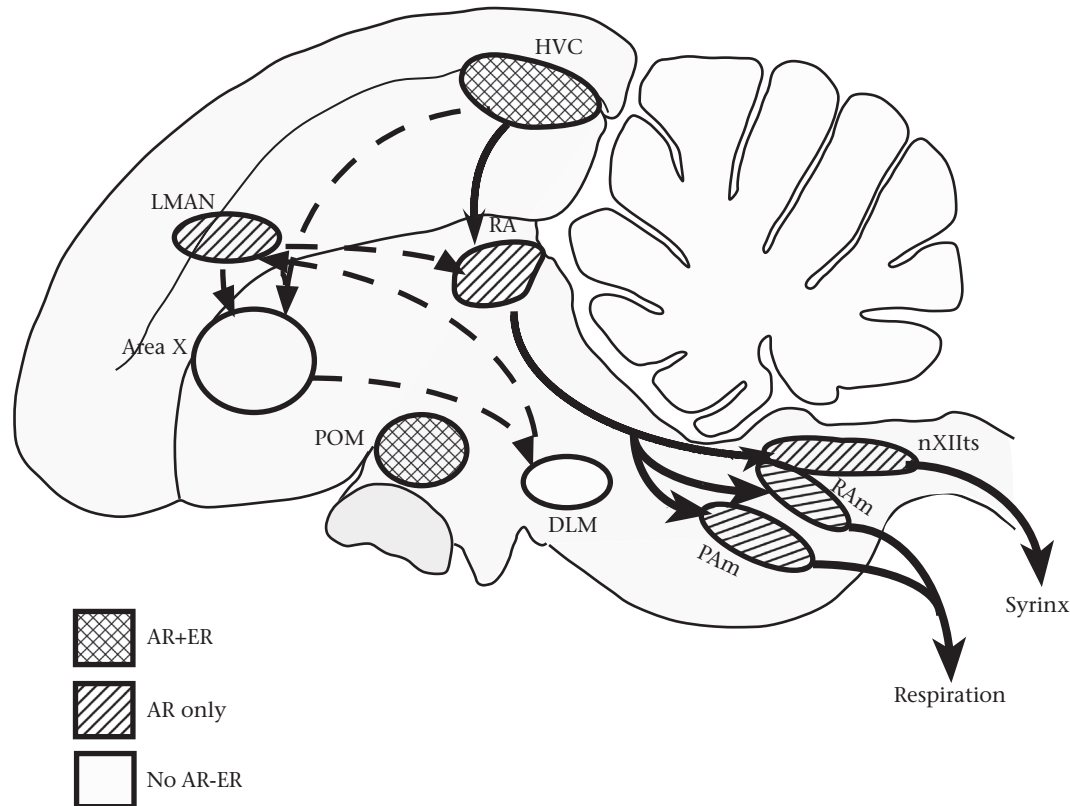


Figure 1. Schematic representation of the song control system of songbirds illustrating the two main pathways connecting nucleus HVC (formerly referred to as the hyperstriatum ventrale pars caudale) to the nucleus robustus arcopallialis (RA). The caudal motor pathway (black solid arrows) directly connects HVC to RA and then to the motoneurons innervating the syrinx located in the tracheosyringeal part of the XIIth cranial nerve (nXIIts) and to two nuclei controlling respiration, the nucleus retroambigualis (RAm) and the nucleus parambigualis (PAm). This pathway is needed for song production, and testosterone action in HVC can be related directly to the quality of song produced. The anterior forebrain pathway (dashed arrows) also connects HVC to RA but via the Area X of the striatum, the dorsolateral thalamic nucleus (DLM) and the lateral magnocellular nucleus of the anterior nidopallium (LMAN). The pathway is necessary for normal song learning and development, and testosterone acting in LMAN may be related to the gating of song variability introduced via the LMAN-to-RA projection. The medial preoptic nucleus (POM) is also represented; although it is not known to connect directly to the song system, testosterone action in this nucleus enhances a general motivation to engage in courtship behaviours, including the motivation to sing. Nuclei that contain nuclear androgen receptors (AR), oestrogen receptors (ER) or no sex steroid receptors are also shown. Membrane receptors for these sex steroids are also present in the avian brain and could participate to song control, but their neuroanatomical distribution is poorly documented at present.

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