

Review article

Endocrine and social regulation of adult neurogenesis in songbirds

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ABSTRACT

The identification of pronounced seasonal changes in the volume of avian song control nuclei stimulated the discovery of adult neurogenesis in songbirds as well as renewed studies in mammals including humans. Neurogenesis in songbirds is modulated by testosterone and other factors such as photoperiod, singing activity and social environment. Adult neurogenesis has been widely studied by labeling, with tritiated thymidine or its analog BrdU, cells duplicating their DNA in anticipation of their last mitotic division and following their fate as new neurons. New methods based on endogenous markers of cell cycling or of various stages of neuronal life have allowed for additional progress. In particular immunocytochemical visualization of the microtubule-associated protein doublecortin has provided an integrated view of neuronal replacement in the song control nucleus HVC. Multiple questions remain however concerning the specific steps in the neuronal life cycle that are modulated by various factors and the underlying cellular mechanisms.

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1. Introduction

Until a few decades ago, the morphology of the brain was thought to be relatively fixed and change very little once an individual had reached adulthood. In particular, the number of neurons in the brain was supposed to be stable among adults. According to this dogma, all mammals, including humans, were born with a set number of neurons and this number was then inexorably set to decrease throughout life with no intervention known that could possibly reverse this trend ((Ramon y Cajal, 1913), cited in (Marler and Slabbekoorn, 2004), p. 258). The discovery of adult neurogenesis in the late 20th century was thus greeted with excitement but also suspicion (Gage et al., 2008a). Studies of songbirds played a significant role in the phenomenon of adult neurogenesis gaining general acceptance in the neuroscience community (Goldman, 2008). Songbirds and other avian species still play a valuable role in studies of the regulation and function of adult neurogenesis as this phenomenon occurs at a high rate in the avian brain and can be studied in songbirds in well defined neural circuits.

In this review, we will first briefly summarize the history of this revolution in the neurosciences and the role played by studies of

songbirds in establishing the acceptance by the neuroscience community of an active process of neurogenesis in the adult brain. We will then focus on seasonal changes affecting the neurogenesis process in songbirds and the different tools that have been used to study this phenomenon. A third section will be devoted to the experimental dissection of the multiple factors that modulate this seasonally variable neurogenesis. A final section will review studies still ongoing that are designed to better characterize the social effects on neurogenesis and the multiple sites of action of testosterone on singing activity and the associated neurogenesis.

2. The song control system

In the early 1970s, Fernando Nottebohm studied possible processes of proprioceptive feedback and discovered that in some songbird species such as canaries the neural control of the syrinx was lateralized ((Nottebohm, 1971; Nottebohm and Nottebohm, 1976); see Nottebohm (1980) for a review). This led to a series of studies with colleagues at the Rockefeller University to analyze the neural mechanisms that control song production in canaries. They discovered based on tract-tracing and lesion experiments a discrete circuitry that controls the learning and production of song, the so-called song control system (Nottebohm, 1980). This discovery laid the foundation for a prolific line of research that has refined the anatomy of the song control system and determined many aspects of its functions (Nottebohm, 2004, 2008) (see

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Ziegler and Marler (2008) for a recent synthesis of this research field) (see Fig. 1).

The learning and production of vocalizations is in songbirds supported by neural specializations that include two interconnected circuits of telencephalic, diencephalic, mesencephalic and myelencephalic nuclei (Brenowitz et al., 1997), a caudal motor pathway mostly involved in song production and a more rostral forebrain pathway mostly involved in song learning and auditory feedback needed to maintain adult song.

The caudal pathway starts at nucleus HVC (initially misnamed as Hyperstriatum Ventrale pars caudale, later called High Vocal Center and now used as a proper name, see: Brenowitz et al., 1997; Reiner et al., 2004; Ziegler and Marler, 2008). HVC projects to the nucleus robustus arcopallialis (RA) that in turn projects to the dorsomedial portion of (DM) of the nucleus intercollicularis (ICo). Both RA and DM then project to several medullary components of this circuit including the tracheosyringeal part of the nucleus of the XIIth cranial nerve (nXIIts) that innervates the vocal production organ the syrinx as well as to two nuclei that coordinate respiration with song production, the nucleus retroambigualis (RAm) and the nucleus parambigualis (PAm) also called rostral Ventral Respiratory group (rVRG) in the older avian literature (Wild, 1994, 2004, 2008; Schmidt and Wild, 2014). Lesions to nuclei in this pathway block song production (Nottebohm et al., 1976; Simpson and Vicario, 1990), and functional studies based on electrophysiology or on the detection of immediate early genes demonstrate that these nuclei are active during song production (Yu and Margoliash, 1996; Jarvis and Nottebohm, 1997; Kimpo and Doupe, 1997).

The more rostral pathway, also called the anterior forebrain pathway also connects HVC to RA but through an indirect route including Area X of the medial striatum, the medial part of the dorsolateral thalamic nucleus (DLM) and the lateral magnocellular nucleus of the anterior nidopallium (LMAN). This pathway is organized as follows HVC → X → DLM → LMAN → RA (Fig. 1). LMAN additionally projects to Area X. This anterior forebrain pathway is critical for song learning (see Bottjer and Johnson (1997) for a review) and for maintaining the stereotyped structure of the adult song. One theory is that this is via an error correction process

(Benton et al., 1998; Brainard and Doupe, 2000; Brainard, 2004; Kao et al., 2005), but lesions to nuclei in this pathway do not immediately alter adult song production (Bottjer et al., 1984; Sohrabji et al., 1990; Scharff and Nottebohm, 1991). What is clear is that the LMAN input into RA injects variability in song essential for sensorimotor song learning (Nottebohm, 2005). LMAN appears to facilitate motor variability via its glutamatergic projections to RA and this results in a functional remodeling of RA circuits that in turn modifies behavioral output (reviewed in Nottebohm, 2005; Brainard, 2008; Schmidt, 2009).

3. Songbirds and the (re)discovery of adult neurogenesis

The first studies describing adult neurogenesis in the mammalian brain were published by Joseph Altman at the Massachusetts Institute of Technology (MIT) in the 1960s. He found evidence for newly born neurons in the adult hippocampus of rats and guinea pigs (Altman and Das, 1965, 1967). These findings were generally ignored (Gross, 2009) since they were contradicting a widely held dogma stating that all neurons in the mammalian brain are produced before or soon after birth (Paton and Nottebohm, 1984; Gross, 2009).

After the discovery of the song system Nottebohm and colleagues identified a number of fascinating brain – behavior correlations namely between variation in the volume of key forebrain song control nuclei and certain measures of song behavior. For example, he found with his student Art Arnold that there are prominent sex differences in the volume of song nuclei that correlate with measures of song output such as the complexity of song structure ((Nottebohm and Arnold, 1976); see MacDougall-Shackleton and Ball (1999) and Ball et al. (2008) for reviews of more recent studies). He reported that the volume of song nuclei within males in canaries and later marsh wrens correlated with the size of the song repertoire (Nottebohm et al., 1981; Canady et al., 1984). This correlation turned out not to be the result of differential learning (Brenowitz et al., 1995) but it nonetheless identified how behavioral variation could relate to variation in the brain, even with a rather crude measure such as brain nucleus volume.

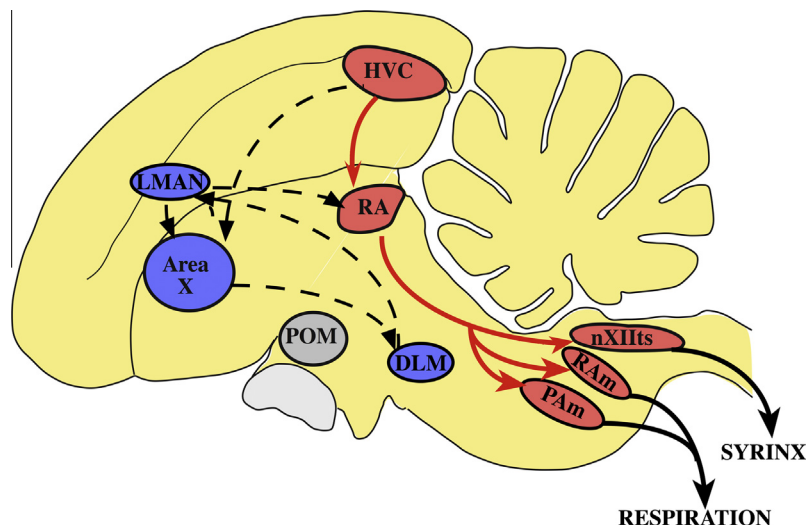


Fig. 1. Schematic representation of the song control system of songbirds illustrating the two main pathways connecting nucleus HVC (initially Hyperstriatum Ventrale pars caudale, now acronym used as proper name) to the nucleus robustus arcopallialis (RA). The caudal motor pathway (solid arrows) directly 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). The anterior forebrain pathway (dotted 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 medial preoptic nucleus is also represented; although it is not known to connect directly to the song system, testosterone action in this nucleus enhances the singing motivation (see Section 14).

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