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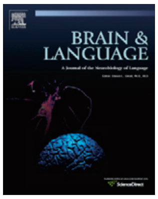

The relationship of neurogenesis and growth of brain regions to song learning

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ABSTRACT

Song learning, maintenance and production require coordinated activity across multiple auditory, sensory-motor, and neuromuscular structures. Telencephalic components of the sensory-motor circuitry are unique to avian species that engage in song learning. The song system shows protracted development that begins prior to hatching but continues well into adulthood. The staggered developmental timetable for construction of the song system provides clues of subsystems involved in specific stages of song learning and maintenance. Progressive events, including neurogenesis and song system growth, as well as regressive events such as apoptosis and synapse elimination, occur during periods of song learning and the transitions between variable and stereotyped song during both development and adulthood. There is clear evidence that gonadal steroids influence the development of song attributes and shape the underlying neural circuitry. Some aspects of song system development are influenced by sensory, motor and social experience, while other aspects of neural development appear to be experience-independent. Although there are species differences in the extent to which song learning continues into adulthood, growing evidence suggests that despite differences in learning trajectories, adult refinement of song motor control and song maintenance can require remarkable behavioral and neural flexibility reminiscent of sensory-motor learning.

1. Introduction

Vocal learning is remarkably similar in songbirds and humans. In both cases, the capacity to learn is constrained by inborn predispositions, relies on hearing, is modulated by social context, and wanes with increasing age. Moreover, even in songbirds that do not normally change their songs in adulthood, the maintenance of song stereotypy, as with speech, is an active process dependent on hearing. Finally, vocal learning in birds and humans relies on a specialized series of brain regions (Doupe & Kuhl, 1999; Kuhl, 2003).

Research over the past two decades has revealed that a substantial amount of avian brain development occurs after hatching and continues well into adulthood. This provides an exceptional opportunity to relate specific developmental neurobiological events to the acquisition and expression of learned vocal behavior. This developmental timetable also raises the possibility that the building and refinement of avian vocal control circuitry is dependent on vocal experience, and there is ample evidence that this is at least partially true. However, growing evidence also suggests that this plasticity is constrained in important ways. The purpose of this review is to provide an outline of what is known about key aspects of brain development as they relate to song learning. While the list of species in which song learning and brain development have been explored is increasing, the most comprehensive analyses have been done on the zebra finch and canary and so much of the work that will be described comes from these two species. However, comparative work incorporating more species has begun to provide important new insights and so, where appropriate, this work will be cited as well.

2. Timetable for song learning

In nearly all oscine songbirds that have been examined, song learning begins when juveniles memorize the songs of one or more adults. Auditory memories are then used to guide vocal motor development during a sensory-motor stage. The sensory-motor phase progresses through several stages beginning with sub-song, which bears little resemblance to adult song, followed by a plastic song stage where individual notes or syllables can be recognized but are highly variable from one song rendition to the next, followed finally by song crystallization, where notes and, in some species, note sequences, are sung in a highly stereotyped manner (see Williams, 2008 for review).

All songbirds studied to date require auditory experience for normal song development and in some species, exposure to song must occur during an early critical period for it to be copied (Konishi, 2004). There is also evidence for a critical period during which

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vocal motor practice is essential in the zebra finch (Pytte & Suthers, 2000). Among songbirds, canaries and zebra finches may represent the extremes on a continuum in terms of song learning. While in both species, song is predominantly or exclusively produced by males, and in both species song is initially learned during juvenile life, these species differ with respect to learning trajectories. The zebra finch is often referred to as ''close-ended'' or ''age-limited'' in that most of song development is over by 90–120 days after hatching, around the time birds reach sexual maturity (Arnold, 1975; Immelmann, 1969). Zebra finch song is comprised of one-to-several short, introductory notes, followed by 4–7 individually distinct and more complex 'syllables' or note complexes, which are typically produced without repetition and in a fixed sequence. This comprises the bird's ''motif'', which can be sung one-to-several times in rapid succession (referred to as a song bout). After puberty, there is very little change in the acoustic structure of individual notes, but occasional variation in note number and sequence persists (Brainard & Doupe, 2001; Glaze & Troyer, 2006; Lombardino & Nottebohm, 2000; Nordeen & Nordeen, 1992, 1993; Williams, 2004; Williams & Mehta, 1999). In contrast, the canary is considered an ''open-ended'' learner. Canaries sing up to 30–40 distinct notes, repeating each several times before transitioning to another, and note sequence is not fixed (Guttinger, 1985; Nottebohm, Nottebohm, & Crane, 1986). Canaries go through a similar early learning sequence (Marler, 1997; Marler & Waser, 1977), but the process of remodeling song continues throughout life on a seasonal basis. Canaries as old as 4–5 years have been known to learn new song from conspecifics (Guttinger, 1979). Song is remodeled by the addition of new syllables as well as the loss or modification of pre-existing syllables. Canaries also retain some syllables from previous years and there may be strain differences in the amount of new song material learned each year (Leitner et al., 2001; Nottebohm et al., 1986; Voigt & Leitner, 2008).

The open-ended versus age-limited classification of these two species is somewhat inaccurate. While it is true that unlike canaries, normally raised zebra finches cannot (or will not) learn to produce the songs of other conspecifics after song crystallization (Eales, 1985; Zevin, Seidenberg, & Bottjer, 2004), zebra finch song note stereotypy increases with adult age (Pytte, Gerson, Miller, & Kirn, 2007) and relies on auditory feedback (Brainard & Doupe, 2000a; Lombardino & Nottebohm, 2000; Nordeen & Nordeen, 1992; Wang, Aviram, & Kirn, 1999; to be discussed in more detail later). Adult song refinement and maintenance may reflect an active process reminiscent of the later stages of juvenile song learning, whereby slight deviations from a target song are corrected based on auditory feedback. In support of this idea, recent work has shown that naturally occurring drift in adult zebra finch song is corrected by re-exposure to the original tutor song (Funabiki & Funabiki, 2008) and that adult zebra finches will alter note pitch to avoid masking white noise (Tumer & Brainard, 2007; also see Sober & Brainard, 2009) Thus, while zebra finches will normally not learn new songs as adults, it is likely that sensory-motor matching and error correction, used in the later stages of juvenile song development, continue well into adulthood. At the other end of the spectrum, song modification in the open-ended canary appears to decrease with adult age (Nottebohm et al., 1986) and a relatively large fraction of the syllables produced in a breeding season were learned at some earlier (perhaps juvenile?) stage in life (Leitner et al., 2001; Nottebohm et al., 1986; Voigt & Leitner, 2008). Although it is clear that adult vocal plasticity in the canary exceeds that in the zebra finch, it seems equally clear that zebra finches retain vocal flexibility after puberty. Moreover, although canaries do modify songs annually, they recycle some previously learned notes. From these behavioral insights, one might also expect more similarities in adult vocal control system plasticity than is implied by the age-limited/open-ended labels.

3. The vocal control system

Arguably the single most important discovery in the history of the songbird field, from a neuroethologist's perspective, was that there is a discrete series of brain regions dedicated to song learning and production (Nottebohm, Stokes, & Leonard, 1976). This provided an unprecedented opportunity to explore the neurobiological control of a single, well-defined and learned behavior in endothermic vertebrates. Subsequent work has added important brain regions to this circuitry and refined functional distinctions. The vocal control system as well as important auditory structures is illustrated in Fig. 1. A timetable for the development of this complete series of brain regions is lacking and so, for the purpose of this review, the focus will be restricted to a few key structures essential for vocal learning and song production. One major pathway, often referred to as the 'motor' pathway, includes two pallial (cortical) structures, HVC (used as a proper name) and RA (robust nucleus of the arcopallium). HVC projects to RA and neurons of this type (HVC⇒RA) make up approximately 60% of all HVC neurons (Alvarez-Buylla, Theelen, & Nottebohm, 1988; Kirn, Alvarez-Buylla, & Nottebohm, 1991; Kirn, Fishman, Sasportas, Alvarez-Buylla, & Nottebohm, 1999). In turn, RA projects directly and indirectly onto brain stem regions innervating respiratory motor neurons, as well as motor neurons innervating the vocal musculature (syrinx). The 'motor' designation is based in part on this anatomical configuration, the fact that the temporal pattern of activity in this pathway closely maps onto and precedes sound production, and also on the fact that lesions at any point within this circuit disrupt adult song production, although deficits vary based on lesion placement (Margoliash, 1997). A second major circuit, referred to as the anterior forebrain pathway (AFP), is analogous to basal ganglia-cortico-thalamic circuitry in mammals (reviewed by Bottjer, 2004). This pathway begins with HVC and a cell population distinct from that synapsing on RA. This latter population (HVC⇒X) projects to a medial striatal region, Area X, which, in turn, projects to the thalamus (DLM, dorsal lateral nucleus of the medial thalamus). DLM then projects to a cortical region called LMAN (lateral magnocellular nucleus of the anterior nidopallium). LMAN projection neurons have bifurcating axons, with one terminal field in Area X and the other in RA (Vates & Nottebohm, 1995). A key feature of these two pathways is that they both have efferent projections originating in HVC that directly or indirectly converge on the dendrites of neurons in RA (Canady, Burd, DeVoogd, & Nottebohm, 1988; Herrmann & Arnold, 1991; Mooney & Konishi, 1991). Lesions within the AFP have modest, if any, effects on fully stereotyped song but severely disrupt vocal development (Bottjer, Miesner, & Arnold, 1984; Kao, Doupe, & Brainard, 2005; Nordeen & Nordeen, 1993; Scharff & Nottebohm, 1991; Sohrabji, Nordeen, & Nordeen, 1990; Williams & Mehta, 1999).

Based on the results from early lesion studies, there has been a strong tendency to parse the two pathways just described into a song production pathway and a learning pathway. While these labels accurately describe essential features of song that require the integrity of the two pathways, several lines of evidence suggest that both pathways are important for sensory-motor learning and song maintenance. For example, there is evidence that both pathways are involved in song production. Neurons throughout both pathways exhibit song-related pre-motor activity and acute, micro-stimulation applied to either pathway during singing alters song structure (Hessler & Doupe, 1999; Kao et al., 2005; Vu, Mazurek, & Kuo, 1994; Yu & Margoliash, 1996). There is also evidence that both pathways serve auditory functions, perhaps related to song learning and maintenance. Under appropriate conditions, neurons in both pathways respond to sound stimuli (reviewed by Doupe, Solis, Kimpo, & Boettiger, 2004) and this is even true of the brainstem motor neurons innervating the syrinx (Williams & Nottebohm, 1985). Moreover, many neurons in both pathways