

## NEUROSCIENCE FOREFRONT REVIEW

# TWO NEURAL STREAMS, ONE VOICE: PATHWAYS FOR THEME AND VARIATION IN THE SONGBIRD BRAIN

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**Abstract**—Birdsong offers a unique model system to understand how a developing brain – once given a set of purely acoustic targets – teaches itself the vocal-tract gestures necessary to imitate those sounds. Like human infants, to juvenile male zebra finches (*Taeniopygia guttata*) falls the burden of initiating the vocal-motor learning of adult sounds. In both species, adult caregivers provide only a set of sounds to be imitated, with little or no information about the vocal-tract gestures used to produce the sounds. Here, we focus on the central control of birdsong and review the recent discovery that zebra finch song is under dual premotor control. Distinct forebrain pathways for structured (theme) and unstructured (variation) singing not only raise new questions about mechanisms of sensory-motor integration, but also provide a fascinating new research opportunity. A cortical locus for a motor memory of the learned song is now firmly established, meaning that anatomical, physiological, and computational approaches are poised to reveal the neural mechanisms used by the brain to compose the songs of birds. © 2014 IBRO. Published by Elsevier Ltd. All rights reserved.

**Key words:** vocal learning, sensory-motor integration, motor memory, premotor cortex, basal ganglia.

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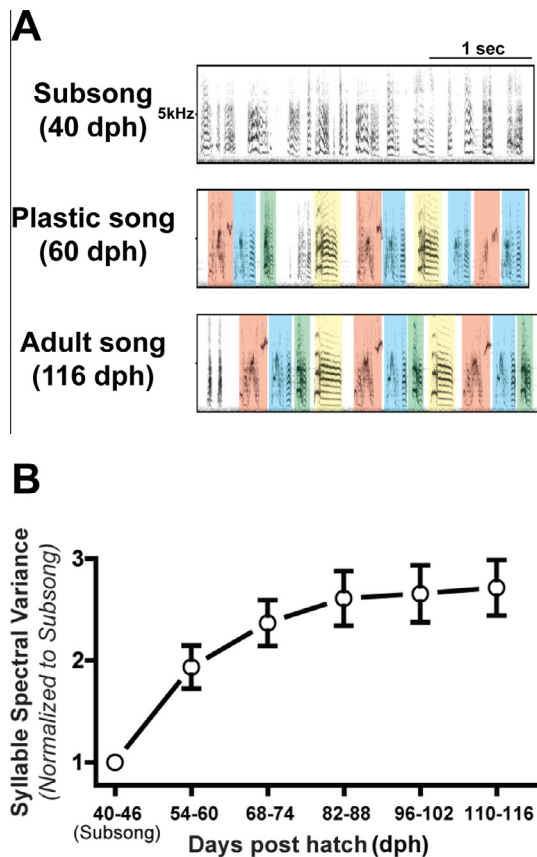
**Abbreviations:** AFP, anterior forebrain pathway; GTE, gesture trajectory extrema; LMAN, lateral magnocellular nucleus of the anterior nidopallium; NIf, nucleus interface; RA, robust nucleus of the arcopallium; Uva, nucleus uvaeformis; VMP, vocal motor pathway.

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## INTRODUCTION

Among various forms of developmentally-regulated learning, birdsong most resembles human speech learning. Similar to human infants, juvenile male zebra finches learn to imitate a paternal vocal pattern in a two-phase process that proceeds with little or no requirement for external reinforcement. The initial ‘sensory’ phase involves the formation of an auditory memory of the paternal vocal pattern. Notably, the memory contains only the product of the paternal vocal behavior – the acoustic structure and sequence of vocal sounds. As with human speech there is minimal transmission of information about how to produce the sounds.

In zebra finches, the subsequent ‘sensory-motor’ stage of learning overlaps the initial sensory stage. Sensory-motor learning begins with highly unstructured singing (termed ‘subsinging’) that resembles the vocal babbling of human infants (see Fig. 1A). As the name implies, sensory-motor learning requires sensory feedback of the juvenile bird’s own vocalizations for song to be learned. Of critical importance is auditory feedback, which references the auditory memory of paternal song acquired during sensory learning (Price, 1979; Funabiki and Konishi, 2003). Interestingly, the variable structure of subsinging appears to be a purposeful exploration of the dynamic range of the vocal organ (Ölveczky et al., 2005; Aronov et al., 2008; Thompson et al., 2011), and perhaps provides a period of associative learning where relationships between different vocal gestures and the sounds those gestures produce are discovered. Subsinging is followed by plastic song, characterized by the emergence of a spectrally-pluripotent class of syllables (protosyllables) that progressively differentiate in a piecemeal fashion into facsimiles of the syllables and syllable sequences present in the paternal song pattern (Tchernichovski et al., 2001; Miller et al., 2010; Ravbar



**Fig. 1.** (A) Frequency spectrograms from 40, 60, and 116 days post-hatch (dph) show the emergence of structured song by a developing male zebra finch. Sensory-motor learning begins with subsong, characterized by unstructured singing that is reminiscent of the babbling of human infants. Individual syllable types (colored transparencies) emerge during plastic song. Adult song is characterized by a fixed repertoire of song syllables that are produced in a canonical sequence – a facsimile of the paternal song pattern heard earlier in life. (B) Quantification of normative vocal development ( $N = 9$  birds, mean  $\pm$  S.E.M.). Relative to undifferentiated subsong syllables, the complexity of syllable spectral structure rises dramatically as birds enter plastic song and plateaus as the adult form is reached. Syllable spectral variance is a composite of variance values for pitch, pitch goodness and entropy, normalized to subsong and averaged. Data are replotted from Elliott et al. (2014) and replicate original findings by Tchernichovski et al. (2001).

et al., 2012; Lipkind et al., 2013 and Fig. 1B). As male zebra finches reach adulthood (90–120 days post-hatch) the song pattern consolidates into a motor memory that is subsequently referenced and produced throughout adult life as a behavioral marker of a bird's paternal lineage.

## THE PREMOTOR CONTROL OF BIRDSONG

The juvenile learning and adult production of birdsong is controlled by a bilateral forebrain network that is remarkable in its anatomical isolation and singular purpose (Fig. 2A). The nodes of this behavioral 'intranet' are distributed throughout avian cortex, basal ganglia, and thalamus. Moreover, with the exception of modulatory (aminergic) and sensory inputs and motor output, these nodes are connected primarily with one

another. Consequently, the learned vocalizations of passerine birds are the product of neural activity in an anatomically private forebrain network that drives a dynamic and quantitatively rich behavior (Fig. 2B, C). The one-to-one correspondence between a forebrain neural network and the complex learned behavior it controls makes the songbird vocal control network a unique experimental platform for elucidating the neural mechanisms of vertebrate learning and memory.

A series of classic circuit-breaking studies (Nottebohm et al., 1976; Bottjer et al., 1984; Simpson and Vicario, 1990; Scharff and Nottebohm, 1991) revealed that the vocal control network contains at least two functionally distinct pathways, termed the vocal motor pathway (VMP) and the anterior forebrain pathway (AFP). The cortical premotor region HVC (proper name, not an acronym) contributes to both pathways and plays a central role in juvenile learning and adult production of song. One population of HVC neurons projects directly to vocal-motor cortex (RA, the robust nucleus of the arcopallium) while a second population projects to the avian basal ganglia (Area X). Both pathways converge at RA (see Fig. 2A) where individual RA neurons integrate synaptic input from HVC and LMAN (the lateral magnocellular nucleus of the anterior nidopallium, Mooney and Konishi 1991; Stark and Perkel, 1999). However, synapse number shifts during the course of vocal learning, favoring LMAN over HVC at the start of sensory-motor learning ( $\sim 9:1$ ), then favoring HVC over LMAN as the adult song emerges ( $> 2:1$ , Herrmann and Arnold, 1991).

While the necessity of the VMP for production of adult song came quickly into focus (Nottebohm et al., 1976; Simpson and Vicario, 1990), developing a clear understanding of the premotor function of the AFP proved somewhat more complex. Disconnecting the output nucleus of the AFP (bilateral ablation of LMAN, see Fig. 2A) produces distinctly different vocal effects, depending on whether a bird is a learning juvenile or a mature adult. LMAN ablation/inactivation during the period of juvenile learning curtails vocal development (Bottjer et al., 1984; Scharff and Nottebohm, 1991; Olveczky et al., 2005; Elliott et al., 2014) whereas LMAN ablation in adulthood initially appeared to be without effect on the structure of adult song (Bottjer et al., 1984; Scharff and Nottebohm, 1991). Experimental evidence that the AFP might make a premotor contribution to adult song arose first in the work of Jarvis and Nottebohm (1997), who demonstrated singing-driven immediate-early gene (IEG) expression in LMAN and Area X of adult birds. Later, Kao et al. (2005) demonstrated that stimulation of LMAN during adult singing induced concurrent shifts in syllable pitch. Subsequent studies demonstrated that the AFP actively contributes a subtle dispersion to the spectral and temporal attributes of adult song syllables produced by the VMP (Kao and Brainard, 2006; Thompson et al., 2011). That is, adult song becomes more structured and less variable following LMAN ablation (see example in Fig. 3). The earlier assessment that LMAN ablation is without effect on adult song is understandable – detecting subtle shifts in the dispersion of

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