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Review Paper

At the interface of the auditory and vocal motor systems: NIf and its role in vocal processing, production and learning

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ABSTRACT

Communication between auditory and vocal motor nuclei is essential for vocal learning. In songbirds, the nucleus interfacialis of the nidopallium (NIf) is part of a sensorimotor loop, along with auditory nucleus avalanche (Av) and song system nucleus HVC, that links the auditory and song systems. Most of the auditory information comes through this sensorimotor loop, with the projection from NIf to HVC representing the largest single source of auditory information to the song system. In addition to providing the majority of HVC's auditory input, NIf is also the primary driver of spontaneous activity and premotor-like bursting during sleep in HVC. Like HVC and RA, two nuclei critical for song learning and production, NIf exhibits behavioral-state dependent auditory responses and strong motor bursts that precede song output. NIf also exhibits extended periods of fast gamma oscillations following vocal production. Based on the converging evidence from studies of physiology and functional connectivity it would be reasonable to expect NIf to play an important role in the learning, maintenance, and production of song. Surprisingly, however, lesions of NIf in adult zebra finches have no effect on song production or maintenance. Only the plastic song produced by juvenile zebra finches during the sensorimotor phase of song learning is affected by NIf lesions. In this review, we carefully examine what is known about NIf at the anatomical, physiological, and behavioral levels. We reexamine conclusions drawn from previous studies in the light of our current understanding of the song system, and establish what can be said with certainty about NIf's involvement in song learning, maintenance, and production. Finally, we review recent theories of song learning integrating possible roles for NIf within these frameworks and suggest possible parallels between NIf and sensorimotor areas that form part of the neural circuitry for speech processing in humans.

Contents

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1. Introduction

Songbirds offer a tremendous opportunity for studying the sensorimotor integration underlying vocal learning. Like humans, oscine songbirds learn to reproduce conspecific vocalizations during development through a process that requires vocal practice and auditory feedback (Doupe and Kuhl, 2008; Tschida and Mooney, 2012). Songbirds evaluate their vocal performance by using auditory feedback from self-produced vocalizations and use this performance evaluation to adjust motor patterns, gradually shaping vocal output to match a stored template of tutor song (Williams, 2008). Thus, song learning is critically dependent on the action and interaction of the auditory and vocal-motor systems. While a great deal of progress has been made towards understanding how each of these systems functions independently, far less is understood regarding the interactions between them that enable song learning and maintenance. Part of the difficulty in understanding these interactions can be attributed to the nucleus that sits at the interface of the auditory and song systems: the nucleus interfacialis of the nidopallium (NIf). Despite numerous studies designed to elucidate the function of NIf and the importance of its sensorimotor input to the song system, the role of NIf in song learning and production remains unclear.

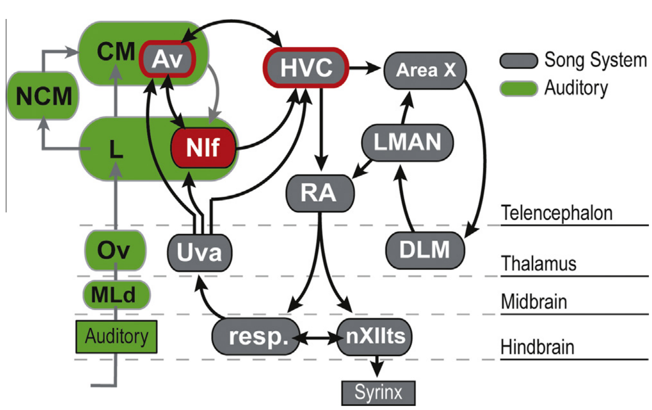

Fig. 1. Auditory and motor pathways in the avian brain. Input from the auditory pathway (shown in green) reaches NIf from CM, particularly through a reciprocal connection with the Av subdivision of CM. Av also shares a reciprocal connection with HVC. The connections between Av, NIf, and HVC form a sensorimotor loop that links the auditory forebrain and the song system (highlighted in red). The descending motor pathway consists of the projection from HVC to RA and the projections from RA onto brainstem respiratory nuclei (resp.) and the tracheosyringeal portion of the hypoglossal nucleus (nXIIts). Whether the projection from NIf to HVC should also be included in the descending motor pathway is not yet clear (see Section 4). Ascending feedback from brainstem vocal and respiratory centers reaches NIf and HVC via the thalamic nucleus Uva. The anterior forebrain pathway (AFP), which is critical for song learning, consists of Area X, which receives input from HVC, the medial nucleus of the dorsolateral thalamus (DLM), and the lateral magnocellular nucleus of the anterior nidopallium (LMAN), which projects to RA. Abbreviations: L: the Field L complex; MLd: dorsal lateral nucleus of the mesencephalon; NCM: caudal medial nidopallium; Ov: nucleus ovoidalis.

In songbirds, higher-order auditory processing occurs in the auditory forebrain by a set of highly interconnected structures organized much like auditory cortex in mammals (Jarvis et al., 2005; Wang et al., 2010). These auditory structures include the Field L complex, the avian homologue of primary auditory cortex in mammals, and secondary auditory areas NCM (caudomedial nidopallium) and CM (caudal mesopallium). Motor production of song in oscine songbirds is controlled by a network of discrete sensorimotor nuclei that are collectively referred to as the song system (Nottebohm et al., 1976, 1982). The song system (Fig. 1) consists of two main pathways: the descending motor pathway and the anterior forebrain pathway (AFP). The descending motor pathway is made up of the telencephalic nucleus HVC (used as a proper name) and its efferent target RA (the robust nucleus of the arcopallium), which sends projections to respiratory and vocal motor nuclei in the brainstem (Wild et al., 2000; Wild, 2004). Converging evidence from lesions (Simpson and Vicario, 1990; Aronov et al., 2008), electrical stimulation (Vu et al., 1994), localized cooling (Long and Fee, 2008; Aronov et al., 2011), and single cell recordings (Hahnloser et al., 2002, 2006) indicate that HVC drives the descending motor pathway to shape many of the spectrotemporal features of song. The anterior forebrain pathway consists of a basal ganglia–thalamo-cortical circuit that indirectly links HVC to RA and is critical for song learning (Brainard and Doupe, 2000a). In addition to these two pathways, the song system also contains two recurrent "thalamocortical" pathways that indirectly link RA back to HVC (Schmidt et al., 2004). One of these pathways provides ascending feedback to NIf and HVC from the vocal-respiratory brainstem via thalamic nucleus uvaeformis (Uva) and is critical for normal song production (Striedter and Vu, 1998; Coleman and Vu, 2005; Ashmore et al., 2008; Akutagawa and Konishi, 2010).

The central location of HVC and its critical importance for song learning and production (Mooney, 2009) have led to numerous studies seeking to understand how activity in HVC influences the activity of other nuclei in the song system. In this review, we focus on NIf, one of the nuclei, which most strongly influences HVC's own neural activity (Cardin and Schmidt, 2004b; Coleman and Mooney, 2004; Cardin et al., 2005). Like other song system nuclei, NIf exhibits both auditory and vocal-motor activity. Auditory activity in NIf is of particular interest because NIf's input to HVC is the largest single source of auditory information to the song system (Vates et al., 1996; Cardin and Schmidt, 2004a; Coleman and Mooney, 2004; Cardin et al., 2005; Bauer et al., 2008). In addition, NIf provides nearly all of HVC's spontaneous excitatory drive (Cardin and Schmidt, 2004a; Cardin et al., 2005), has premotor bursts that precede similar bursts in HVC (McCasland, 1987; Lewandowski and Schmidt, 2011), and drives the replay of premotor-like bursting in HVC during sleep (Hahnloser and Fee, 2007). Given the critical necessity of HVC for song learning and production,