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A species-specific view of song representation in a sensorimotor nucleus

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ABSTRACT

Songbirds constitute a powerful model system for the investigation of how complex vocal communication sounds are represented and generated, offering a neural system in which the brain areas involved in auditory, motor and auditory–motor integration are well known. One brain area of considerable interest is the nucleus HVC. Neurons in the HVC respond vigorously to the presentation of the bird's own song and display song-related motor activity. In the present paper, we present a synthesis of neurophysiological studies performed in the HVC of one songbird species, the canary (*Serinus canaria*). These studies, by taking advantage of the singing behavior and song characteristics of the canary, have examined the neuronal representation of the bird's own song in the HVC. They suggest that breeding cues influence the degree of auditory selectivity of HVC neurons for the bird's own song over its time-reversed version, without affecting the contribution of spike timing to the information carried by these two song stimuli. Also, while HVC neurons are collectively more responsive to forward playback of the bird's own song than to its temporally or spectrally modified versions, some are more broadly tuned, with an auditory responsiveness that extends beyond the bird's own song. Lastly, because the HVC is also involved in song production, we discuss the peripheral control of song production, and suggest that interspecific variations in song production mechanisms could be exploited to improve our understanding of the functional role of the HVC in respiratory–vocal coordination.

1. Introduction

The neural processing of acoustic communication signals is crucial for survival and social interactions in vocal species. Over the last two decades, evidence for the idea that a specialization for processing complex vocalizations emerges through an hierarchy of auditory areas has been accumulating. In songbirds, neurons in secondary auditory forebrain areas, which are analogous to the secondary auditory cortex in mammals, respond more strongly to songs of other individuals of the same species (conspecifics) than to other complex stimuli (Chew et al., 1996; Stripling et al., 1997; Theunissen et al., 2004; Theunissen and Shaevitz, 2006), and may even develop response biases towards learned songs (Gentner and Margoliash, 2003; Jeanne et al., 2011). Beyond these auditory areas, the brain nuclei involved in singing and song learning have provided one of the most striking examples of highly selective responses. In adult songbirds, they fire more to the presentation of the bird's own song (BOS) than to conspecific song or even to the BOS played in reverse (Margoliash, 1983; Margoliash and Fortune, 1992; Lewicki and Konishi, 1995; Mooney, 2000; Rosen and Mooney, 2003). The sensorimotor nucleus HVC (used as a proper name) was the first song nucleus in which song-selective neurons were observed. This nucleus receives both direct and indirect auditory inputs, has been implicated in song perception (Brenowitz, 1991; Gentner et al., 2000), is necessary for song production (Nottebohm et al., 1976; Simpson and Vicario, 1990), and is thought to establish the correspondence between the auditory and motor representations of a vocalization (Prather et al., 2008) (see below).

Over the past 30 years, most studies of the song selectivity of HVC neurons have been performed in species that sing a single song, such as the white-crowned sparrow (*Zonotrichia leucophrys*) or the zebra finch (*Taenopygia guttata*) (Margoliash, 1983, 1986; Margoliash and Fortune, 1992; Theunissen and Doupe, 1998; Mooney, 2000), and more recently, in a species that sings 2–5 simple song types, the swamp sparrow (*Melospiza georgiana*) (Mooney et al., 2001; Prather et al., 2008). Some of these studies have provided evidence that song selectivity includes responses not only to particular syllables within a song, but also to combinations of syllables presented in a specific temporal order. Modifying the song strikingly affects auditory responsiveness, revealing the precision with which the temporal and spectral structure of the syllable needs to be preserved (Margoliash and Fortune, 1992; Theunissen and Doupe, 1998). The HVC contains projection neurons and inter-

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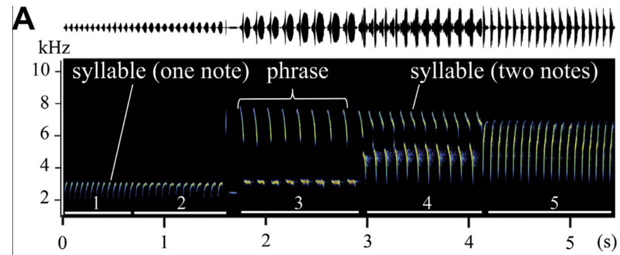
neurons, which differ in their degree of selectivity: projection neurons are more narrowly tuned than interneurons (Mooney, 2000; Mooney et al., 2001; Coleman and Mooney, 2004). In the swamp sparrow, which has a small number of song types, each consisting of the repetition of a single syllable, single HVC projection neurons often respond to the playback of only a single song type; among these neurons, those that project to Area X are capable of exhibiting both motor-related activity and auditory responses to a playback of the BOS (Mooney et al., 2001; Prather et al., 2008). In contrast, a single interneuron can respond to all of the bird's song types (Mooney et al., 2001). BOS-selectivity does not arise in the HVC, but an enhancement of auditory selectivity does occur at this site. *In vivo* intracellular recordings have revealed that the local HVC circuitry transforms broadly-tuned auditory inputs into a more BOS selective song representation in the HVC, through interactions between excitatory and inhibitory mechanisms (Rosen and Mooney, 2003).

Studies conducted in species that sing a single song or a limited number of song types have deepened our understanding of how the BOS is processed in the HVC. However, recent studies in other songbird species have expanded this picture and provided new insights into the neural coding of song in the HVC by investigating the auditory properties of HVC neurons, addressing scientific questions that cannot be addressed (or that have not been addressed) in species such as the zebra finch. By taking advantage of species-specific aspects of song acoustics or song-related behavior, these studies have begun to examine the relationship between the auditory properties of HVC neurons and song features and suggest that the strategy used to encode song in the HVC may vary, to a certain extent, among songbird species (Nakamura and Okanoya, 2004; George et al., 2005a; Nealen and Schmidt, 2002, 2006).

Songbird species show great diversity in nearly all aspects of song, including the extent to which song behavior changes with season, the repertoire size of song elements or of song types, song element ordering and the peripheral control of song production (Nealen and Schmidt, 2002; Brenowitz and Beecher, 2005). This article provides a synthesis of studies from our laboratory concerning the neural representation of song in the HVC of the anesthetized canary (*Serinus canaria*), a species which presents a set of song-related behaviors in natural contrast to those of the zebra finch. Briefly, male canaries, which produce fairly complex songs, are well known for their pronounced seasonal changes in both song behavior and song structure, providing an opportunity to ask whether HVC neurons modify their selectivity to match changing song structure. To determine whether seasonal plasticity alters how the BOS is encoded in the HVC, selectivity for the forward BOS over the reverse version was first evaluated using the firing rate as a metric and then by quantifying the information conveyed by spike trains. Then, the selectivity of HVC neurons in canaries under breeding conditions was used to examine how, in a songbird species in which both song structure and the encoding of individual identity are complex, an individual's song is distinguished from conspecific songs. Finally, because the HVC lies at the confluence of the auditory and motor streams (Nottebohm et al., 1976; McCasland and Konishi, 1981) and is currently considered a site where precise auditory–vocal correspondence is established (Prather et al., 2008), the question of how birds produce their song was considered to shed light on interspecific differences.

2. Song structure in the canary

The canary has a fairly complex song structure (Güttinger et al., 1978). Canary song consists of a series of phrases, where each phrase is composed of the repetition of a syllable generally formed of 1 or 2 notes (Fig. 1). A male canary has a repertoire of around 20–30 distinct phrases (range 12–40). Only a part of the repertoire (on average, 8–10 phrases) is present in each song, and phrases may be recombined in different ways (Fig. 1B). There is thus no fixed repertoire of song types. However, some phrases do occur in a relatively fixed order, forming sequences of a given number of phrases ("*n*," varying from 2 to 6) that regularly occur in songs of the same individual (Del Negro et al., 2005; Lehongre et al., 2008). The succession of phrases in a song is probably constrained by some form of syntactic organization. The most frequently delivered sequence of n phrases appears more often than might be expected based on the overall frequency of its constituent phrases (Lehongre et al., 2008).



B

Song n°	1	2	3	4	5	6	7	8	9	10	11
	1	1	1	1	7	2	2	1	1	1	1
	2	2	2	2	16	3	3	2	2	2	2
	3	7	3	3	17	4	4	19	19	19	19
	4	8	4	4	10	5	5	4	4	4	4
	5	18	5	5	15	6	6	5	5	5	13
	6	4	6	6	8	10	10	6	6	6	5
		9	10	10	18	11	8	15	15	15	6
			15	11	19	12	18	8	8	8	8
				12	9	15	4	18	18	18	10
				15	12	20	9	11	9	11	11
				8	15	13	14	20	14		12
				18	8	18					15
				4	18	19					21
				13	5	9					
					6	21					

Fig. 1. Structure of a canary song. (A) Sound oscillogram (representation of time vs. sound pressure; top) and spectrogram (representation of time vs. frequency; bottom) of one song of a given male. Canary songs consist of a series of phrases, with each phrase composed of a syllable repeated multiple times. The different phrase types of the individual's repertoire are numbered. (B) Table showing how distinct phrases of the repertoire of a given bird were delivered within 11 songs of a given bird. Phrases were labelled individually. The three most recurrent sequences of six phrases and their sub-sequences are indicated in gray. The representative song selected as the BOS stimulus is the song no. 4. Both its oscillogram and its sonogram are shown in Fig. 3D.

Canary songs likely provide information as to the identity of the singer. Female canaries display more sexual behavior in response to their mate's song than to songs of other males, even if they have been previously familiarized to the non-mate song (Beguin et al., 1998). Males trained in a discrimination-learning task accurately discriminate between songs produced by two different birds (Appeltants et al., 2005). The song of an individual possesses several distinctive features that can potentially be used to recognize the singer (Lehongre et al., 2008). In the phrase repertoire of each individual, only a few phrases (range: 2–6) are specific to the bird, with the majority of phrases being shared by two or more males living in the same or in a different aviary (Lehongre et al., 2008, 2009). Two familiar males may share up to 70% of their repertoire, while this value is around 50% for two unfamiliar males (Lehongre et al., 2009). The phrases in the repertoire of an individual also differ in the frequency of their occurrence. Therefore, even if two