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Mechanisms of song perception in oscine birds

Daniel P. Knudsen [a], Timothy Q. Gentner [b,*]

[a] *Neurosciences Graduate Program, University of California, San Diego, La Jolla, CA 92093, United States*

[b] *Department of Psychology, University of California, San Diego, La Jolla, CA 92093, United States*

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ABSTRACT

Songbirds share a number of parallels with humans that make them an attractive model system for studying the behavioral and neurobiological mechanisms that underlie the learning and processing of vocal communication signals. Here we review the perceptual and cognitive mechanisms of audition in birds, and emphasize the behavioral and neural basis of song recognition. Where appropriate, we point out a number of intersections with human vocal communication behavior that suggest common mechanisms amenable to further study, and limitations of birdsong as a model for human language.

1. Introduction

Like other communication signals, one adaptive function of birdsong is to influence the behavior of others, usually conspecific individuals (Kroodsma & Miller, 1996). Communication signals achieve this function by transmitting information between the sender of the signal and the receivers. The success of this transmission rests on predictability. When a sender produces a specific signal, in this case a song, it does so under the expectation that the signal will elicit a predictable (i.e. intended) behavior in the receiver. Without the predictable correspondence between production and perception, signals would lose their functionality. Thus, the presence of a functional signal implies a reliable correspondence between production and perception mechanisms shaped and maintained by selection pressures. This correspondence confers a special status to communication signals. Like other natural stimuli, communication signals are often physically complex. Unlike most complex natural stimuli, however, many of the physical dimensions along which communication signals vary can be directly tied to adaptive behaviors. Research in oscine birds has capitalized on this idea to study the mechanisms underlying the perception and cognition of complex natural stimuli (song) in the context of natural behaviors.

What follows is an account of our current understanding about the ways in which the songbird auditory system interprets a continuous stream of acoustic information as a collection of behaviorally relevant communication signals and uses this information to affect behavior (Fig. 1). Parallels will be drawn to human vocal communication, and we will present a case for the use of songbirds as a model of certain aspects of human language processing. We first provide a broad overview of perceptual psychophysics in songbirds so that one can appreciate the strong perceptual similarities between birds and humans. We then review the behavioral and neurophysiological work on conspecific song perception, focusing on individual vocal recognition mechanisms in European starlings, a species of songbird.

2. Perceptual psychoacoustics

It is helpful for any description of a complex system to begin with a characterization of general abilities along fundamental dimensions. Common dimensions along which acoustic signals are deconstructed are frequency, amplitude, and time, and it is instructive to understand sensory processing at this level. The goal of such research is to inform our understanding of how more 'atomic' descriptions of sounds give rise to the perception of more complex behaviorally relevant features. Such studies provide an important context for studies of more complex signals, and establish the range over which any perceptual ability can operate. The following section provides a brief description of avian psychoacoustics studies supporting the notion that humans and birds experience a similar acoustic world. More thorough reviews are available (Dooling, 1982, 1992, 2000; Fay, 1988).

* Corresponding author. Address: UCSD, Department of Psychology, 9500 Gilman Dr. MC0109, La Jolla, CA 92093-0109, United States.
E-mail address: tgentner@ucsd.edu (T.Q. Gentner).

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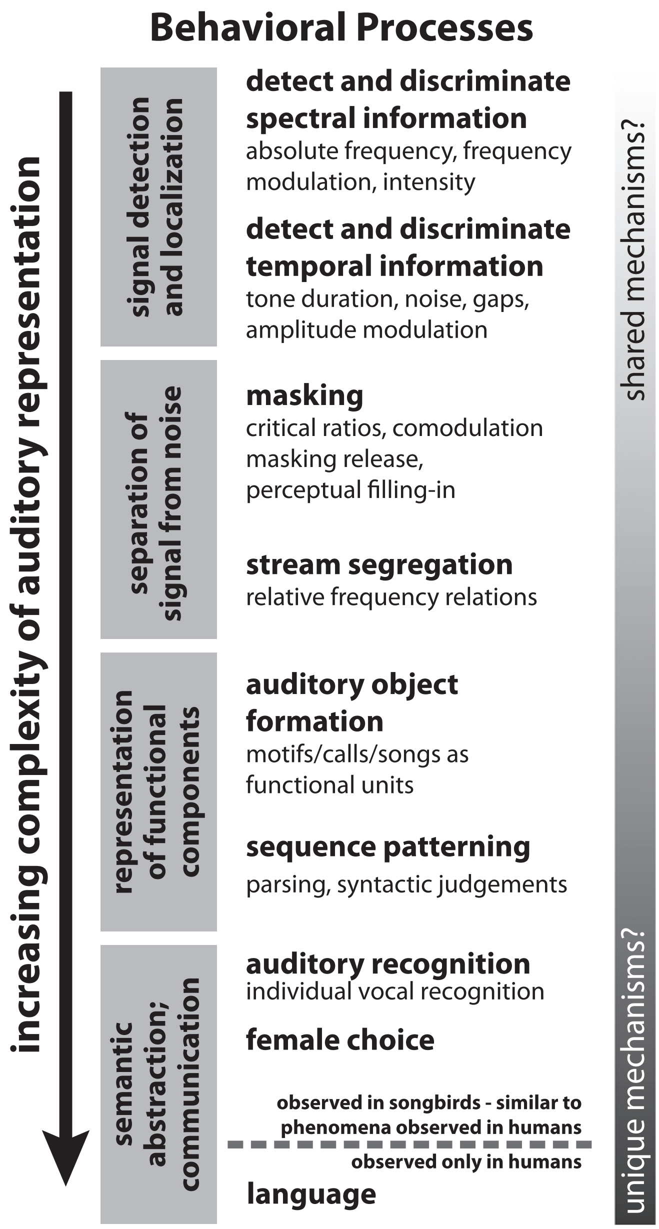

Fig. 1. Functional auditory behaviors in songbirds. The gray boxes represent the functions that the auditory system must perform to mediate behavior. Text to the right of these functions gives examples of phenomena observed in songbirds (see text). Although this review focuses on songbird auditory processing, many of the functions of the auditory system are likely conserved across a range of vertebrates, including humans. As behavioral complexity increases, so does the likelihood that particular mechanisms are unique to different species. The similarities and the differences between species yield powerful comparative hypotheses about the behavioral and neural mechanisms for auditory perception and cognition in vertebrates.

2.1. Spectral sensitivity

Audibility curves, which describe the loudness (sound pressure level, SPL) required for detectability as a function of frequency, have the same basic shape in many songbird species (Dooling, Okanoya, Downing, & Hulse, 1986; Okanoya & Dooling, 1987). The threshold sensitivity for pure tones in most songbird species is best around 2–5 kHz, increases gradually as the frequency of the tone becomes lower, and increases quite sharply as the frequency of the tone rises. The typical high-frequency cutoff for songbirds is 8–11 kHz. Although audibility thresholds are lower in humans than in birds, the overall shape of the audibility curve is similar.

In addition to hearing single tones, the auditory system must also discriminate between different tones. Understanding the minimal detectable differences between tones can point to the types of frequency modulations within a signal that are available for a species to use in vocal communication. In general, birds are quite sensitive to changes in frequency, and can discriminate a change in frequency as small as 1% (Dooling, 1982), while humans have even lower detection thresholds across the range of audible frequencies. Birds' sensitivity to frequency changes also depends on the type of frequency modulation and range of carrier frequencies (Langemann & Klump, 1992), results again similar to observations made in human studies (Demany & Semal, 1989; Fastl, 1978). To detect a change in intensity (loudness) between two successive tones, birds require a difference of about 3 dB, humans about 1 dB (Dooling, 1982). While humans have quantitatively lower detection thresholds for frequency and loudness discrimination, the similarity of findings in humans and birds point to auditory systems that are qualitatively similar in the range of psychophysically observable spectral sensitivities.

2.2. Temporal sensitivity

Most acoustic signals unfold over time, and processing in the temporal domain is therefore particularly important. Temporal processing abilities of songbirds have been studied in a variety of ways. A simple measure is the detectability of a sound as its temporal duration increases. In general, the longer the tone is played for, the lower the SPL needed for detection. Consistent with findings from a host of other animals including humans (see Brown & Maloney, 1986), birds' thresholds for hearing a pure tone improve as the duration is increased from a few milliseconds to 200–300 ms (Dooling, 1980). Another common measure of temporal acuity, known as the gap detection threshold, measures the minimum temporal interval that can be detected between two sounds. Several studies from birds show gap detection thresholds ranging from 2 to 3 ms, which is similar to thresholds found in humans (see Klump & Maier, 1989). This suggests that intervals in natural vocalizations less than 2–3 ms may not be perceived. Duration discrimination measures, which describe an organism's ability to determine whether one sound has a longer duration than another, are also similar between birds and humans (Maier & Klump, 1990).

2.3. Masking

In psychoacoustics, the critical ratio describes the ability of an organism to perceive a tone in a noisy background. It is defined as the SPL of a target tone needed for detection divided by the SPL of the background masking noise. Critical ratios are a function of the frequency of the target tone, and in accordance with previous studies in humans and in other mammals, critical ratios in most songbirds increase at about 3 dB per octave (Dooling et al., 1986; Langemann, Klump, & Dooling, 1995; Okanoya & Dooling, 1987). Most songbirds' critical ratio curves show a similar shape to those of humans and other mammals, though humans show lowered threshold levels on the order of a few decibels (Okanoya & Dooling, 1987).

Comodulation masking release (CMR) is a slightly more complex masking phenomenon that has been described in both birds and humans. CMR occurs when sounds that are modulated together across time serve to release each other from masking by overlapping noise. CMR is measured as the effective decrease in threshold SPL afforded by the comodulation. CMR has been proposed as mechanism for auditory stream segregation (discussed below), as sounds that are produced from the same source take the same path to the listener and are therefore modulated