



A comparative analysis of auditory perception in humans and songbirds: A modular approach



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ABSTRACT

We propose that a relatively small number of perceptual skills underlie human perception of music and speech. Humans and songbirds share a number of features in the development of their auditory communication systems. These similarities invite comparisons between species in their auditory perceptual skills. Here, we summarized our experimental comparisons between humans (and other mammals) and songbirds (and other birds) in their use of pitch height and pitch chroma perception and discuss similarities and differences in other auditory perceptual abilities of these species. Specifically, we introduced a functional modular view, using pitch chroma and pitch height perception as examples, as a theoretical framework for the comparative study of auditory perception and perhaps all of the study of comparative cognition. We also contrasted phylogeny and adaptation as causal mechanisms in comparative cognition using examples from auditory perception.

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At the core of the study of comparative cognition is the question of how best to study similarities and differences in cognitive abilities among species. Researchers have noted similarities worth exploring between human speech and music on the one hand and birdsong on the other (Doupe and Kuhl, 1999).

Both humans and songbirds learn their vocalizations early in life, exhibit a strong dependence on hearing the adults they will imitate, as well as hearing themselves as they practice, and exhibit a diminished dependence on these models as they mature. Innate predispositions for perceiving and learning the correct sounds exist in both groups. Humans also share with songbirds an early phase of learning that is primarily perceptual, which then serves to guide later vocal production. Both humans and songbirds have evolved a complex hierarchy of specialized forebrain areas in which motor and auditory centers interact closely. (Paraphrased from Doupe and Kuhl, 1999).

Here, we use a modular approach to compare some of the most important auditory skills in the perceptual toolkits humans and songbirds use to perceive and produce their communication systems. We ask how animals use their auditory skills to produce and perceive their vocalizations. By this we mean that a species auditory toolkit is a critical determinant of its auditory

communication. For example as a first approximation, the toolkit for humans must include neural machinery for perception of relative pitch, pitch height, pitch chroma, temporal duration, rhythm, and tempo (some of the definitions follow and Burns (1999) provides further definitions).

The goal is to use the present work to provide examples of a modular approach to the study of comparative cognition. Some would insist on an extensive *a priori* definition of modules (e.g., Fodor, 1983). We have a different view; functional modules are products of evolution and obey no *a priori* rule except natural selection (Barrett and Kurzban, 2006). We are aware of the controversy over modules and think it unhelpful, especially in the case of perceptual modules. Readers who wish to consider the controversy further are referred to Barrett and Kurzban's (2006) extensive discussion.

We describe comparisons between humans and songbirds in two common and powerful auditory perceptual abilities: perception of pitch height and of octave equivalence. Pitch height is a log-linear scale of pitch where the greater the difference between two frequencies, the greater the difference in perceived pitch. When a doubling or halving of frequency separates two successive sounds, humans can perceive this unique relationship as octave equivalence. In musical terms, notes played at the same chroma (relative position) in different octaves can be perceived as similar, that is, equivalent in chroma. Pitch chroma perception is always a cognitive skill because it requires categorization of pitches based

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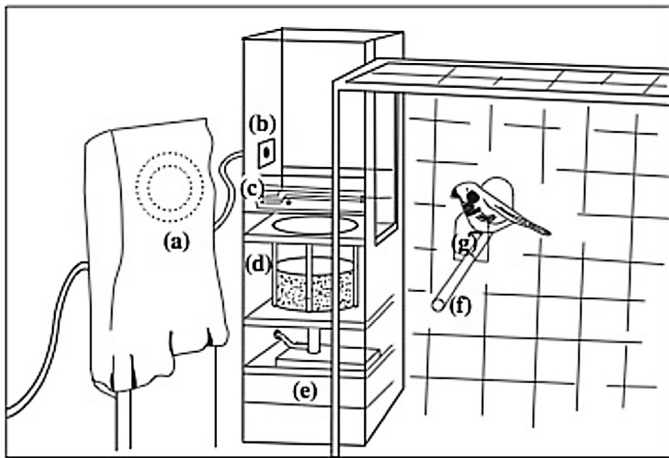


Fig. 1. Schematic of songbird operant chamber: (a) Speaker, (b) red LED, (c) infrared sensors on feeder, (d) feeder cup, (e) feeder drive motor, (f) request perch, (g) infrared sensor assembly, and male zebra finch on request perch. For clarity, other perches, water bottles, etc. are not drawn here. Redrawn from Fig. 1 in [Sturdy and Weisman \(2006\)](#).

on a common feature. Pitch height perception can require only the decision that one pitch is higher than another, but as a cognitive skill requires categorization of contiguous pitches as sharing a common outcome, as in categorizing voices as adult male or female. Here to avoid long windy definitions, we simply refer to these pitch categorizations as pitch height and pitch chroma perception.

Pitch height and pitch chroma can be seen as opposing percepts. To a listener attending to pitch chroma, pitches with a frequency relationship of 1:2 seem more similar than those that share a relationship of 3:4; for a listener attending to pitch height, the opposite would be true. In humans, both abilities are important in speech and music ([Burns, 1999](#)). Later, we will briefly touch on relative pitch and note timing, which are also important to human and songbird communication.

In trying to make sense of published findings about similarities and differences among species in their auditory skills, we have developed a modular theory of comparative auditory cognition, which might apply quite generally. We freely admit being influenced by current research in neuroscience ([Wagner et al., 2007](#)) and evolutionary psychology ([Barrett and Kurzban, 2006](#)) in our thinking about a modular view of the mind and the brain. Our working assumption is that cognition consists mainly of the operation of fairly simple and independent modules, which by their operation or lack thereof account for differences in the cognitive abilities of various species. We will have more to say about the theory as we describe our findings about the comparative cognition of auditory perception. Most important, we will introduce our adaptation of some basic neuroscience tools to study the comparative science of cognition.

1. Laboratory protocols for the study of auditory perception in songbirds and humans

We used operant discrimination tasks to evaluate perceptual functioning across species. We show the songbird testing apparatus in [Fig. 1](#). The main features of the songbird testing apparatus are: (i) a monitored perch the birds use to trigger the presentation of acoustic stimuli, (ii) a monitored, motorized feeder, and (iii) a high-quality speaker ([Sturdy and Weisman, 2006](#)). The human testing apparatus was a laptop computer and a pair of high-quality over-the-ear headphones ([Hoeschele et al., 2012](#)). In research with rats (*Rattus norvegicus*; [Weisman et al., 2004](#)) and pigeons (*Columba livia*; [Weisman et al., 2010b](#)), standard operant chambers were

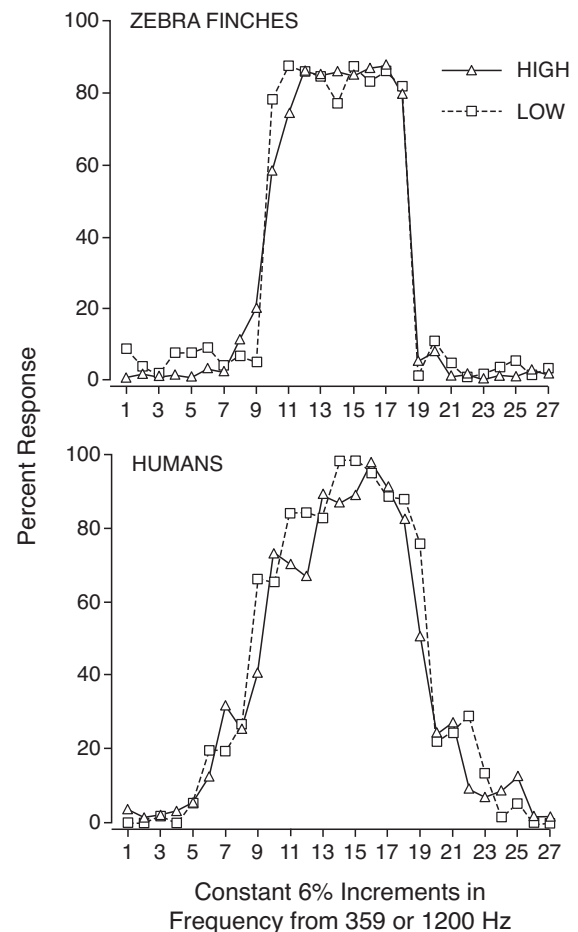


Fig. 2. Mean Percentage of response across constant 6% increments in frequency from 359 or 1,200 Hz in the low- and high-frequency ranges, respectively, in the final session of the three-frequency range discrimination for zebra finches (upper panel) and humans (lower panel). Zebra finches gave 95% and humans gave 85% of their responses to S+ tones. Reproduced from [Fig. 2](#) in [Weisman et al. \(1998\)](#).

used with high-quality speakers. In experiments with songbirds, pigeons, and rats, the rewards were foods appropriate to the species; in experiments with humans, positive feedback and competitive rewards were standard.

Laboratory protocols are important to the extent that they illuminate how animals use their cognitive skills in their daily lives; the assumption is that expert abilities shown in the laboratory translate to highly adaptive behavior in nature. However, field research must always be used to support laboratory findings.

2. Discriminations based on pitch height perception

We began our studies of pitch height perception with a well-known Australian songbird, the zebra finch (*Taeniopygia guttata*; [Weisman et al., 1998](#)) and we expanded to studies of many other birds and mammals (see [Weisman et al., 2004](#)). In two experiments, we compared songbirds and humans in their ability to sort frequencies into ranges. In one experiment (see [Weisman et al., 1998](#), Experiment 1), we divided 27 tones, beginning at either 359 Hz or 1,200 Hz and increasing 6% from one tone to the next into three ranges of nine tones each. Tones in lower and upper ranges were not rewarded (no-go or S– tones) and tones in the middle range were rewarded (go or S+ tones). Training continued for 5,000–7,000 trials in both species.

A second experiment (see [Weisman et al., 1998](#), Experiment 2) grouped pitches in a rough approximation of the ranges of

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