



## Biological salience influences performance and acoustic mechanisms for the discrimination of male and female songs



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### ARTICLE INFO

#### Article history:

Received 1 December 2014

Initial acceptance 12 January 2015

Final acceptance 27 February 2015

Available online 12 May 2015

MS. number: A14-00974R

#### Keywords:

acoustic discrimination  
artificial neural network  
black-capped chickadee  
categorization  
female song  
operant conditioning  
vocal communication

In temperate songbirds, song is traditionally considered a reproductive and territorial signal produced by males. Previous research has described the production of male and female songs by black-capped chickadees, *Poecile atricapillus*, a temperate songbird species. Statistical classification revealed that the frequency decrease in the first note of the song is a potential acoustic mechanism that would allow birds to distinguish between the sexes. Here we used an operant discrimination task to examine whether this statistical difference in song is an acoustic difference that is perceived by black-capped chickadees in a manner that would allow birds to quickly assess the sex of a singing conspecific. To better understand the underlying perceptual mechanisms for this sex-based discrimination, we also presented birds with untrained, manipulated songs. In experiments 1 and 2, we tested black-capped chickadees using a true category/pseudo category task. Birds in a true category group performed similarly to birds in a pseudo category group, suggesting that there is no advantage in discrimination abilities for birds using categorization (i.e. true category group) over rote memorization (i.e. pseudo category group), possibly because the heightened biological salience of the song influenced the performance of the chickadees. However, responses to untrained songs suggest that birds learned a sex-based category rule when discriminating among songs. In experiment 3, we trained artificial neural networks (ANNs) using an analogous task in order to examine responding in the absence of experiential or biological factors. Results from ANNs suggest that male and female songs are acoustically distinct and can be discriminated using categorization, and that acoustic features within the first note are an important acoustic mechanism for this sex-based discrimination. Overall, the results suggest that the biological salience of the songs affected the birds' responses.

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Darwin (1859) proposed the theory of sexual selection, describing males as the sex that produces elaborate traits for male–male competition or mate attraction. Male birdsong offers an example of elaborate traits arising through a process of sexual selection: males produce songs to advertise territory to rival males and attract females (for review see Catchpole & Slater, 2008). However, male songbirds are not the only sex that produces songs. In the tropics, female song production is common (Slater & Mann, 2004), and while it is frequently stated that only male songbirds produce songs in north temperate-zone species (reviewed in: Langmore, 1998; Riebel, 2003), recent evidence suggests that

female song is common (Garamszegi, Pavlova, Eens, & Møller, 2007; Odom, Hall, Riebel, Omland, & Langmore, 2014).

The ability to discriminate between male and female songs is important for songbirds, as the information contained within songs varies with the producer of the acoustic signal and the intended receiver (e.g. mate attraction versus territoriality). For songs to be effective as communication signals, the receiver needs to recognize and respond appropriately to the acoustic signals (e.g. mate recognition: Lind, Dabelsteen, & McGregor, 1996; recognition of territory neighbours: Brooks & Falls, 1975). In order for birds to discriminate between male and female songs, the songs must contain discriminable acoustic features. Differences in the singing behaviour and song structure of male and female songs are evident in various species (e.g. white-crowned sparrows, *Zonotrichia leucophrys*: Baptista, Trail, DeWolfe, & Morton, 1993; bellbirds, *Anthornis melanura*: Brunton & Li, 2006; European robins, *Erithacus*

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*rubecula*: Hoelzel, 1986; European starlings, *Sturnus vulgaris*: Pavlova, Pinxten, & Eens, 2005). Even for species in which males and females produce acoustically similar vocalizations, it would be advantageous for birds to quickly assess the sex of a singing individual.

Open-ended categorization (as described by Herrnstein, 1990) is a strategy that allows individuals to classify signals based on perceptual similarity. With open-ended categorization, animals can learn a general 'category' rule for all signals containing perceptually similar features. For example, 'chick-a-dee' calls have been shown to belong to open-ended categories based on the species producing the call (e.g. mountain chickadee, *Poecile gambeli*, calls versus black-capped chickadee, *Poecile atricapillus*, calls; Bloomfield, Farrell, & Sturdy, 2008). With open-ended categorization, birds can discriminate between species based solely on vocalizations and without prior experience with the calling individual. Open-ended categorization would also allow birds to rapidly evaluate the sex of a singing individual, classify the signal according to sex of the singer and generalize unfamiliar songs. The rationale for using open-ended categorization rather than rote memorization for successful discrimination is that if signals are more perceptually similar to other signals within the same group or category, an individual can form a general rule to classify signals into that category. In contrast, to discriminate via rote memorization, an individual must have experience with and memorize all exemplars. If the signals to be discriminated do not contain a discernible feature that allows them to be categorized, rote memorization must be used. Because rote memorization requires memorization of each signal, while open-ended categorization does not, open-ended categorization is a more flexible cognitive process.

In order for open-ended categorization to be an effective strategy, songs must contain at least one feature that is more similar within each category than between categories. Operant discrimination tasks have provided evidence that songbirds use open-ended perceptual category mechanisms to discriminate biologically important acoustic signals, such as conspecific vocalizations (e.g. European starlings: Braaten, 2000; Gentner & Hulse, 1998; zebra finches, *Taeniopygia guttata*: Sturdy, Phillmore, Price, & Weisman, 1999; black-capped chickadees and mountain chickadees: Bloomfield & Sturdy, 2008). However, to our knowledge, no studies have used this type of task to examine the perceptual categorization of songs based on sex of the singer.

Recently it was reported that both male and female black-capped chickadees produce songs (Hahn, Kryslar, & Sturdy, 2013) and that these songs induce different amounts of immediate early gene expression, depending on the sex of the bird producing the song and the sex of the bird hearing the song (Avey, Kanyo, Irwin, & Sturdy, 2008). Black-capped chickadee songs are a relatively simple two-note, tonal signal called the fee-bee song and the songs produced by males and females contain overall structural similarity (i.e. songs of each sex are tonal and contain two notes; Hahn, Kryslar, et al., 2013). The first note in the song (i.e. fee note) is produced at a higher frequency relative to the second note (i.e. bee note), and, across song renditions, males are able to maintain a consistent relative frequency between the two notes (Horn, Leonard, Ratcliffe, Shackleton, & Weisman, 1992; Weisman, Ratcliffe, Johnsrude, & Hurly, 1990). Although the songs produced by males and females are acoustically similar overall, there is at least one acoustic feature that differs between the sexes, called the fee glissando (Hahn, Kryslar, et al., 2013). The fee glissando is a frequency decrease within the fee note and is highly stereotypic in male songs (Christie, Mennill, & Ratcliffe, 2004). The fee glissando is an important acoustic cue for the perception of song; flattening the fee glissando in male songs results in less aggressive responses from rival males (Shackleton, Ratcliffe, & Weary, 1992) and fewer

copulation solicitation displays from females (Ratcliffe & Otter, 1996). Male fee-bee songs are used to attract mates and repel rival males, so the ability to quickly identify the sex of a singing individual would be beneficial, thus saving time and energy trying to mate with the wrong sex or repelling a potential mate. A category perception-like mechanism would allow birds to determine the sex of a vocalizing bird without previous experience with that individual and before visual contact is available.

In the current study, we use an operant go/no-go paradigm to examine (1) whether male and female songs belong to acoustic categories that black-capped chickadees can perceive, and (2) the underlying proximate mechanisms of this sex-based discrimination. In experiments 1 and 2, we trained black-capped chickadees on an operant discrimination task and tested the birds using songs in which we manipulated acoustic features. We were interested in examining whether these birds use acoustic features in one or both notes within the song, and specifically whether the birds use the fee glissando when discriminating between the sexes. In experiment 3, we trained artificial neural networks (ANNs) using the same stimuli that the birds discriminated in experiment 2. We trained ANNs in order to clarify the results from the first two experiments, using a model that does not have any biological confounds. Ultimately, this work will provide valuable insights into the perceptual mechanisms behind a sex-based discrimination of songs in this species, and these results will also add to a growing body of literature on female song in a temperate songbird species.

## EXPERIMENT 1

### Methods

#### Subjects

Seventeen black-capped chickadees (eight males and nine females, identified by DNA analysis; Griffiths, Double, Orr, & Dawson, 1998) were tested between December 2012 and April 2013. Birds at least 1 year of age (determined by examining the colour and shape of their outer tail retrices; Pyle, 1997) were captured in Edmonton (North Saskatchewan River Valley, 53.53°N, 113.53°W; Mill Creek Ravine, 53.52°N, 113.47°W), Stony Plain (53.46°N, 114.01°W) or Kananaskis Country (51.02°N, 115.03°W), Alberta, Canada between January 2010 and February 2012.

Prior to the experiment, birds were individually housed in Jupiter Parakeet cages (30 × 40 × 40 cm, Rolf C. Hagen, Inc., Montreal, QB, Canada) in colony rooms containing other black-capped chickadees. Birds had visual and auditory, but not physical, contact with one another. Birds had ad libitum access to food (Mazuri Small Bird Maintenance Diet; Mazuri, St Louis, MO, U.S.A.), water (vitamin-supplemented on alternating days; Prime Vitamin Supplement; Hagen, Inc.), grit and cuttlebone. Birds were given three to five sunflower seeds daily, one superworm (*Zophobas morio*) three times a week, and a mixture of greens (spinach or parsley) and eggs twice a week. Birds were maintained on a light:dark cycle that mimicked the natural light cycle for Edmonton, Alberta, Canada.

Throughout the experiment, birds were housed individually in operant chambers (see Apparatus below), maintained on the natural light cycle and had ad libitum access to water (vitamin-supplemented on alternate days), grit and cuttlebone. Birds were given two superworms daily (one in the morning and one in the afternoon). Food (i.e. Mazuri) was only available as a reward for correct responding during the operant discrimination task. Birds had previous experience discriminating synthetic tones or musical chords and other fee-bee song stimuli (Hahn, Guillette, Hoeschele, & Sturdy, n.d.; Hahn, Hoeschele, et al., n.d.; Hoeschele, Cook, Guillette, Hahn, & Sturdy, 2014; Hoeschele, Weisman, Guillette, Hahn, & Sturdy, 2013), but no operant experience with the

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