Using network models of absolute pitch to compare frequency-range discriminations across avian species

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\textbf{Abstract}

The spectral frequency ranges of song notes are important for recognition in avian species tested in the field. Frequency-range discriminations in both the field and laboratory require absolute pitch (AP). AP is the ability to perceive pitches without an external referent. The authors provided a network model designed to account for differences in AP among avian species and evaluated it against discriminative performance in eight-frequency-range laboratory tests of AP for five species of songbirds and two species of nonsongbirds. The model's sensory component describes the neural substrate of avian auditory perception, and its associative component handles learning of the discrimination. Using only two free parameters to describe the selectivity and the sensitivity of each species' auditory sensory filters, the model provided highly accurate predictions of frequency-range discrimination in songbirds and in a parrot species, but performance and its prediction were less accurate in pigeons: the only species tested that does not learn its vocalizations. Here for the first time, the authors present a model that predicted individual species' performance in frequency-range discriminations and predicted differences in discrimination among avian species with high accuracy.

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1. Introduction

Birds and mammals are rarely without a voice, and their vocalizations are of demonstrable importance in communication among members of the same species (termed conspecifics). Natural selection has experimented with vocal communication learned by imitation in only a tiny number of distantly related orders and suborders of birds and mammals. Among birds, only true songbirds (oscines), humming birds (Apodiformes), and parrots (Psittaciformes) learn their vocalizations. Among mammals, only whales and dolphins (Cetaceans), bats (Chiroptera), elephants (Elephantidae Loxodonta), and of course humans (Homo sapiens) learn their vocalizations. Comparisons in communication between vocal learning and nonlearning species, and comparisons among vocal learning species are the most powerful tools comparative scientists can apply to understand the evolution of communication (see Jarvis, 2006, for a review). In this article, we have focused on the perceptual basis of vocal communication in birds, and especially in oscines. The flexibility and subtlety of oscines' learned songs and calls are important determinants of oscines' success as a suborder. In fact, oscines are highly successful; they constitute roughly half of the approximately 9000 living species of birds.

1.1. Auditory perception in song playback experiments

Bird songs are most commonly studied in playback experiments conducted in the field. In a playback study, territorial males hear songs either recorded from conspecifics or synthesized to resemble conspecifics' songs. The quantification of vigorous male territorial responses (e.g., approaches to the loud speaker) measures the potency of the perceptual features or characteristics of songs manipulated during playback experiments. Playback studies measure the biological importance of a song's perceptual features directly in nature, without any laboratory artifice. There are hundreds of published studies of song playback in dozens of oscine species (see McGregor, 1992; Slater, 2003). From these field experiments, it is now well known that songbirds collect information about several perceptual features of songs (e.g., number of notes, note duration, and the harmonic structure of notes) in order to identify conspecifics (e.g., Nelson, 1988). In studying this vast literature, it became apparent to our research group...
that one song feature, the spectral frequency ranges of song notes, has been cited repeatedly as important to both individual recognition and species recognition. That is, in field playback experiments, frequency range predominates over other acoustic features (e.g., the timing of notes) in determining the strength of the territorial response (see Nelson, 1989a; Weary et al., 1986). The finding that the frequency range of song notes (typically from the lowest to the highest peak frequency) is important to conspecific recognition has been replicated in at least 12 oscine species (e.g., Dabelsteen and Pedersen, 1985; Emlen, 1972; Falls, 1963; Nelson, 1989b; Lohr et al., 1994; Nowicki et al., 1989; Thompson, 1969; Weary et al., 1986; Weisman and Ratcliffe, 1989; Wunderle, 1979). In a particularly cogent example, Nelson (1989a) demonstrated that field sparrows’ (Spizella pusilla) songs—pitch-shifted upward in frequency by two standard deviations—elicit no more territory defense than songs recorded from birds of other species, whereas songs played back within the normal frequency range elicited vigorous territory defense.

In describing the results of playback studies, field biologists like to talk about the acoustic properties of song, one of which is the ranges of spectral frequencies found in a species’ songs in nature. Be aware, however, that it is not what songbirds sing but what they hear that determines responsiveness to song. What songbirds hear are pitches in response to the frequencies produced in song. This is not a trivial point; the relationship between frequencies and pitches varies between avian and mammalian species, and among avian species, as a function of differences in auditory neurobiology. The critical perceptual ability that enables songbirds to sort song notes into frequency ranges is called absolute pitch (AP). AP is defined as the ability to reproduce or classify pitches with high accuracy without an external referent (Ward, 1998). Songbirds need no pitch pipe or other external standard to identify frequency ranges of the notes in conspecific songs.

1.2. AP and frequency-range discriminations

Although song playback research remains the best method for establishing the importance of a perceptual feature to song recognition, the methodology has several limitations when the goal is to study the perceptual abilities (here AP) that support use of pitch in songs and calls. For example, in playback experiments, birds habituate to extensive and repeated exposure to the same vocalizations and fail to respond at all to simplified acoustic stimuli that do not resemble conspecifics’ vocalizations. In studies of auditory perception, one often wishes to study the responses of individuals across repeated presentations of an array of stimuli. In our AP studies, we present auditory stimuli at different frequencies and compare species in their AP abilities, but we used operant reinforcement techniques to minimize habituation.

Our research group (see Weisman et al., 2006 for a summary) has developed a suite of operant discrimination tasks that provide direct and comparable quantitative measures of frequency-range discrimination across several species of birds. Sturdy and Weisman (2006) have described our laboratory operant equipment and procedures for songbirds in detail. In brief, a bird hears an acoustic stimulus (here always a sinewave tone) presented via a speaker after the bird lands on a monitored perch in a sound isolation chamber. If the stimulus is an S+ (a go stimulus), then flying or hopping from the perch to a feeder is reinforced with food; if the stimulus is an S− (a no-go stimulus), then hopping to the feeder is not reinforced with food and is punished by a delay before the next trial. Pigeons were tested in standard operant chambers fitted with pecking keys and grain feeders (see Friedrich et al., 2007). The pigeons pecked the left key to hear a tone stimulus. If the stimulus was an S+, then pecking the right key was reinforced with food, if the stimulus was an S−, then pecking was punished with a delay. Notice that only pigeons (Columba livia) were trained to key peck.

Frequency-range discriminations are laboratory analogues to identify the frequency ranges of successive notes in conspecific songs in playback experiments. We trained songbirds in the most difficult of these discriminations, the eight-frequency-range discrimination, using 40 tones, spaced 120-Hz apart, in the spectral region between 980 and 5660 Hz, and parsed into eight ranges of five tones each (see Table 1). In the S+ (odd) version of the task, responses (hopping or flying to the feeder) to tones in the odd ranges (1st, 3rd, 5th, and 7th) were reinforced (with food) and responses to tones in the even ranges were not reinforced. In the counterbalanced, S+ (even), version of the task, responses to tones in the even ranges (2nd, 4th, 6th, and 8th) were reinforced. Here we report on performance only in the S+ (odd) version of the discrimination, because performance in the S+ (even) version is virtually the mirror image of performance in the S+ (odd) version.

Over frequency-range experiments, testing a wide range of species, important facts have emerged. The first finding is that birds (for example, zebra finches, Taeniopygia guttata) succeed in accurately tracking every shift between reinforcement and nonreinforcement across eight frequency ranges, whereas humans and rats (and perhaps other mammals) seem only to track the shift from the 1st to the 2nd range and from the 7th to the 8th range but otherwise fail in the eight-range discrimination. The second finding is that, although avian species always track reinforcement across frequency ranges, the accuracy of the discrimination varies considerably across species (Weisman et al., 2006; Friedrich et al., 2007).

2. A network model for classification by AP

The purpose of the present article was to provide a general array model to account for differences among avian species in their ability to sort frequencies into pitch ranges in operant discriminations and, by extension, in territorial defense and mate attraction in nature. Our model has a sensory component that describes the basic neural substrate of avian auditory perception and an associative or learning component that describes how the sensory array is connected to the outcome unit that controls behavior.

<table>
<thead>
<tr>
<th>Frequency range</th>
<th>S+ (go)</th>
<th>S− (no-go)</th>
<th>Frequency (Hz)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>S+</td>
<td>980</td>
<td>1100</td>
</tr>
<tr>
<td>2</td>
<td>S−</td>
<td>1580</td>
<td>1700</td>
</tr>
<tr>
<td>3</td>
<td>S+</td>
<td>2180</td>
<td>2300</td>
</tr>
<tr>
<td>4</td>
<td>S−</td>
<td>2780</td>
<td>2900</td>
</tr>
<tr>
<td>5</td>
<td>S+</td>
<td>3380</td>
<td>3500</td>
</tr>
<tr>
<td>6</td>
<td>S−</td>
<td>3980</td>
<td>4100</td>
</tr>
<tr>
<td>7</td>
<td>S+</td>
<td>4580</td>
<td>4700</td>
</tr>
<tr>
<td>8</td>
<td>S−</td>
<td>5180</td>
<td>5300</td>
</tr>
</tbody>
</table>

Table 1 Frequencies (Hz) of S+ (go) and S− (no-go) tones in the eight-frequency-range discrimination (Weisman et al., 1998).
2.1. The sensory component

We have anchored our sensory array model on the well-known architecture of auditory areas of the avian brain (Miller and Leppelsack, 1985). Tonotopic representations of pitch are seen in the auditory units found in Field L, the surrounding caudal medial nidopallium (NCM), and the caudomedial mesopallium (CMM). In the tonotopic maps, the anatomical position of auditory units is correlated to their pitch response properties, and these networks are the principal means whereby avian brains extract pitch information from auditory signals. In our model, the auditory units are integrated into a tonotopic gradient according to the mid-frequency of effective stimuli (e.g., tones, or noise bands).

Our starting point in modeling the avian anatomical network was Shepard and Kannappan’s (1991) model for stimulus generalization among pitches, which our research group (Njegov et al., 1995) adopted to provide predictions of three-range frequency discriminations in zebra finches. Moore and Glasberg (1987) concluded that the spread of activation across a network of auditory filters is Gaussian, not exponential as Shepard and Kannappan (1991) suggested. Following Moore and Glasberg (1987), we have used a Gaussian model for the pattern of activation across auditory receptor units to provide highly accurate predictions of three- and eight-frequency-range discriminations in zebra finches (see Weisman et al., 1998).

Shepard and Kannappan (1991) used a multi-layer model, with no connections from filter to filter (not feed-forward architecture). We tested single- and multi-layer models. In our multi-layer models sensory units at each level were connected directly to sensory input, with activation controlled by location (see Shepard and Kannappan’s (1991), Fig. 1). Multi-layer models provided no greater precision in predicting performance than a single layer of receptors, so here we report only on the latter. The sensory units in current model are laid out as a row (a single layer connected further by solid lines in Fig. 1). The pitch preferred by a receptor, \( \mu \), corresponds to the receptor’s position in the row: low-frequency pitches at the left and high-frequency pitches at the right. The receptor units illustrated in Fig. 1 serve as band-pass filters, each tuned to a preferred pitch. When a tone is sounded, the preferred units and those nearby become active. Activation in units horizontally adjacent to the preferred receptor is proportional to the ordinate of a Gaussian distribution centered at the preferred receptor.

We assume that each receptor is a constant relative distance, \( D \), from the adjacent receptors, and \( D \) maps onto the species’ primary auditory area, Field L. Given the receptors are equally spaced, we set \( D \) to a standard distance of 1. Hence, to calculate activation, one needs only a single parameter: the standard deviation, \( \sigma \), of the Gaussian distribution. We used \( \sigma \) as a parameter of the model; that is, ordinate values of the filters were a function of \( \sigma \). Put simply, the effective width of the filters varies inversely with \( \sigma \).

Activation, \( A_\mu \), in the receptor aligned at the preferred pitch, \( a_\mu \), is equal to the ordinate of the Gaussian at 0:

\[
A_\mu = N(0, \sigma).
\]

Activation, \( A_j \), in the receptor aligned adjacent to the preferred receptor, \( a_j \), is:

\[
A_j = N(|j|, \sigma),
\]

where \(|j|\) indicates the absolute value of the deviation from the mean in ordinal units and \( A_j \) indicates activation at the receptor \( a_j \) (see Fig. 1). In the model, as the frequency of the preferred pitch increases, activation produced across receptors, decreases according to a geometric function. The geometric function is discrete (the exponential function is the continuous form). Notice that the reduction in the sensitivity of our filters at higher frequencies maps to the well-known reduction in auditory sensitivity with increasing pitch in songbirds (Dooling et al., 2000). Two parameters control activation in the following equation. The first parameter, \( B \), is a value of activation at the base frequency in the array. The second, \( S \), is a sensitivity-reducing multiplier for successive frequencies. We defined values of the geometric function, \( G \), for successive values of \( x \) as:

\[
G(x) = B \times S^x, \quad x = 1 \ldots 100.
\]

The equation shows the calculation for an ordinal set of \( x \) terms (\( x = 1 \ldots 100 \)). The ordinal set of \( x \) terms can be used to describe the intensities of any range of frequencies by varying \( B \) and \( S \) to select the appropriate values. We held \( B \) constant and used \( S \) as a free parameter to fit the decrease in sensitivity with increasing pitch in different species.

2.2. The learning component

Each receptor unit in the array is connected to the outcome (response–reinforcer) unit. Only connections to the outcome unit are modifiable during training. The strength of the connection to the outcome unit from each receptor in the filter array is defined by a weight (\( W \)). We used \( W \) to index the connection to the outcome unit, \( O \), from the receptor at the \( j \)th pitch in the filter array (see Fig. 1). Once training has been completed, the weights are fixed, and the model is ready for testing. In practice, one can alternate between training and testing the model.
When a training tone is presented, activation of the filter array is set by the values associated with the tone. The weights from each unit in the filter array to the outcome unit are changed on each training trial. The change depends on a unit’s current activation, \( A_j \), the nature of the feedback associated with the training trial (positive or negative). First, consider the change, \( \Delta \), associated with feedback. If the feedback is positive (excitatory), the weight is increased by a factor equal to \( \lambda_+ \):

\[
\Delta = A_j \times \lambda_+
\]

If the feedback is negative (inhibitory), the weight is decreased by a factor equal to \( \lambda_- \):

\[
\Delta = A_j \times \lambda_-
\]

The weights themselves are updated as a function of \( \Delta \). Specifically, on successive training trials, the weights are changed using a squash function,

\[
W_j = W_j + \frac{1}{1 + e^{-\Delta}}
\]

where \( e \) is the base of the natural logarithms.

2.3. Predicting discriminative performance

Once training is complete, the activation of the outcome unit in response to the \( j \)th tone, \( O_j \), is set by summing the activation from the filter array weighted by the connection values determined by learning:

\[
O_j = \Sigma(W_j \times A_j).
\]

The values of the outcome unit represent the association between the tones as discriminative stimuli and the response–reinforcer association.

We have assumed a linear relationship between the value of \( O_j \) and actual performance in the frequency-range discrimination. That is, final performance in the discrimination, obtained at each tone, was estimated using simple linear regression, with predicted performance as the output of the network. Predicted performance, correlations, between obtained and predicted values, and root mean square (RMS) estimates of error were calculated from a regression analysis for each species.

3. Using the network model to describe species differences

The model includes seven parameters. Five parameters remained constant across species: (1) the number of stimuli; in the present eight-range discriminations, the number of stimuli = 40, (2) we set \( B \), the value of activation at the base frequency in the array = .25, and the two learning parameters (3) \( \lambda_+ = .300 \) and (4) \( \lambda_- = .050 \). In dozens of tests, across species, wide variation in these parameters was without notable effect. The number of layers, \( \sigma \), and \( S \) were first fit by the Downhill Simplex Method for multi-dimensional minimization, taking the usual precautions to avoid
local minima (Nelder and Mead, 1965; also see Press et al., 1992 for a sample subroutine). As noted earlier (5) one-layer models yield as accurate fits as multi-layer models: so across species, all our predicted values for the percentages of response are for one-layer versions of the model.

We fit the data to obtain values for the final two parameters for seven avian species, five species of songbirds (see Fig. 2) and two nonsongbird species (see Fig. 3). Table 2 lists the sample sizes and Simplex fits for (6) $\sigma$, and (7) $S$; the only parameters found to vary across species. The discrimination data shown in Figs. 2 and 3 were reported by Weisman et al. (2006) and Friedrich et al. (2007).

Results for male and female songbirds were pooled in Fig. 2, except the data for zebra finches were plotted separately. Unlike the other species, female zebra finches were noticeably less accurate than males and are shown separately in Fig. 2. Sex differences in the frequency-range discriminations of male and female zebra finches reflect well-known differences in zebra finch neural song systems (Bailey and Wade, 2003; Nottebohm and Arnold, 1976). As shown in Fig. 2, across species, correlations between obtained and predicted frequency-range discriminations were very high, ranging from >.92 to >.99. Also, RMS error (root mean square error) between predicted and obtained discrimination performance was small across species. On this basis, we concluded that our network model provides an excellent account of AP in the frequency-range discriminations of individual species of songbirds.

We also examined predictions from the model for two nonsongbird species: budgerigars (Melopsittacus undulatus) and pigeons (see Table 2 and Fig. 3). In common with songbirds, both nonsongbird species tracked reinforcement across frequency ranges, although pigeons were less accurate than budgerigars. As shown in Fig. 3, the correlation between obtained and predicted frequency-range discrimination performance was higher and RMS error lower for budgerigars than for pigeons. Variability in discriminative performance across pigeons and mainly poorer accuracy (see results for individual pigeons plotted in Friedrich et al.’s, 2007, Fig. 9) are likely causes of the poorer fit between pigeon performance and the network model.

Also unlike the other species, pigeons were tested using the key-pecking response. In pigeons at least, key pecking for food can be less sensitive to control by auditory than visual stimuli (see Foree and LoLordo, 1973). More recently, Panilillo and Weiss (2005) have suggested that the affective state (positive or negative) associated with the auditory stimulus determines the strength of the association between it and a reinforcer. Alternatively, powerful Pavlovian associations between pecking a visual stimulus and food may hinder operant associations with an auditory stimulus. To test these ideas, we suggest training pigeons, and a few other species that do not learn their vocalizations, in operant auditory tasks that reinforce perching rather than pecking responses. Without discounting these methodological issues, we suggest that the most likely reason for the difference in the models for pigeons and budgerigars is that budgerigars (in common with other parrots and songbirds) learn their calls from conspecifics in adolescence (Farabaugh et al., 1994), whereas pigeons (in common with other columbines) show no evidence of learning their calls (Baptista and Abs, 1983). Despite a poorer predictive fit to pigeons’ performance, as we discuss shortly the model was still useful in predicting species differences in AP.

In Table 2, we show the mean percentage correct across the 40 tones for each species. The percentage correct was calculated as an average of the percentage response on go trials and 100% – the percentage response on no-go trials. We also show the sensitivity, $\sigma$, and selectivity, $S$, parameters fit separately for each species. One might expect that birds that are selective (their auditory receptors are well tuned to the target stimuli, i.e., have a smaller $\sigma$) and whose receptors maintain sensitivity, remain selective even at higher frequencies (i.e., have a higher $S$) would be most accurate at discriminating frequency ranges, tone-by-tone. We computed step-wise regression to determine whether our fitted values of $\sigma$, and $S$ contributed to accurate prediction of overall performance across species. We found that $\sigma$, and $S$ both contributed significantly ($F_{2,7} = 37.12$, $p = .001$) to the prediction of overall accuracy as measured by the mean percentage correct among species ($R_{2,7}^2 = .968$). In other words, the parameters fit by our model accurately predicted differences in discriminative performance among species. Our use of step-wise regression is not an example of data dredging; only two parameters were fit separately to each species and both contributed significantly to the prediction of species differences in the discrimination. This analysis demonstrates the usefulness of formal modeling to comparative cognition by providing specific parametric values for the comparison, and in the present study, a network model generated parameters that described differences between AP across avian species remarkably well.

### Table 2

Species tested: zebra finches (male and females shown separately), white-throated sparrows (females only), black-capped chickadees (males and females pooled), mountain chickadees (males and females pooled), boreal chickadees (males only), budgerigars (males only), and pigeons (males only). Sample sizes, overall percentages correct, and values for the two free sensory receptor parameters in the network, $\sigma$ (selectivity), and $S$ (sensitivity), that predicted species differences are shown.

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>% correct</th>
<th>$\sigma$</th>
<th>$S$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Finch males</td>
<td>4</td>
<td>83.2</td>
<td>0.4768</td>
<td>0.9665</td>
</tr>
<tr>
<td>Finch females</td>
<td>4</td>
<td>79.9</td>
<td>0.5296</td>
<td>0.9861</td>
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<tr>
<td>Sparrows</td>
<td>5</td>
<td>71.7</td>
<td>0.4953</td>
<td>0.9665</td>
</tr>
<tr>
<td>Black capped</td>
<td>8</td>
<td>76.0</td>
<td>0.4998</td>
<td>0.9815</td>
</tr>
<tr>
<td>Mountain</td>
<td>8</td>
<td>71.4</td>
<td>0.4911</td>
<td>0.9610</td>
</tr>
<tr>
<td>Boreal</td>
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<td>60.7</td>
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</tr>
<tr>
<td>Budgerigars</td>
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<td>72.5</td>
<td>0.5394</td>
<td>0.9995</td>
</tr>
<tr>
<td>Pigeons</td>
<td>5</td>
<td>60.8</td>
<td>2.5217</td>
<td>1.0049</td>
</tr>
</tbody>
</table>
4. Conclusions

Here we evaluate our network model using criteria suggested by Guilhardi and Church (2009). Briefly, they proposed that useful quantitative models of behavior should be evaluated against three standards; they must be adequate, simple, and general. Of course, these standards are relative: it is problematic to estimate how adequate, simple, or general a model must be to provide a veridical explanation of behavior.

By adequate, Guilhardi and Church (2009) meant the model must accurately predict behavior. Our network model provided highly accurate predictions of performance in frequency-range discrimination tests of absolute pitch in six avian species. Predictions for pigeon's performance were less accurate but still useful. Further research is needed to determine whether a methodology that avoids the key peck response might improve discrimination but it seems likely that avian species that do not learn to imitate conspecifics have less accurate AP than species that learn their vocalizations through imitation.

Guilhardi and Church (2009) seem to agree with the statement (usually attributed to Albert Einstein) that scientific theories should be made as simple as possible, but not simpler. Complexity is a virtue when it leads to unexpected generality by accounting for more features of behavior, and simplicity is not helpful when it ignores empirical data. Thus simplicity, sometimes called parsimony, must be measured against congruence with known facts about neural architecture and function. Our network model embodies the tonotopic structure of auditory representation in avian brains. If we have erred, it is in making our network simpler than necessary—for example, the model would need to be expanded to handle the representation of the harmonic acoustic signals sometimes observed in oscine songs and calls.

Guilhardi and Church (2009) described important tests of the generality of a model. Generality across samples from the same subjects is a useful check, but generality across species, as obtained here, is an even better test of the generality of our network model. Generality across procedures is another test. We have studied birds in go, no-go discriminations and now suggest that an extension to choice tasks would be a useful test of the generality of our models. Under the generality topic, we should consider its opposite: falsification. Our model is subservient to the theory that accurate AP for pitch range is a generalized avian perceptual ability. If further research, either in the field or in the laboratory, found wide-scale exceptions to the theory, the value of the model would be diminished accordingly. Clearly, further tests of the generality of the model will be useful. On balance, however, frequency-range discriminations and network models of their results have provided a useful account of the predominance of pitch and pitch-range perception in the recognition of vocalizations in birds.

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