

Frequency-Range Discriminations and Absolute Pitch in Black-Capped Chickadees (*Poecile atricapillus*), Mountain Chickadees (*Poecile gambeli*), and Zebra Finches (*Taeniopygia guttata*)

Tiffany T. Y. Lee, Isabelle Charrier, and
Laurie L. Bloomfield
University of Alberta

Ronald G. Weisman
Queen's University

Christopher B. Sturdy
University of Alberta

The acoustic frequency ranges in birdsongs provide important absolute pitch cues for the recognition of conspecifics. Black-capped chickadees (*Poecile atricapillus*), mountain chickadees (*Poecile gambeli*), and zebra finches (*Taeniopygia guttata*) were trained to sort tones contiguous in frequency into 8 ranges on the basis of associations between response to the tones in each range and reward. All 3 species acquired accurate frequency-range discriminations, but zebra finches acquired the discrimination in fewer trials and to a higher standard than black-capped or mountain chickadees, which did not differ appreciably in the discrimination. Chickadees' relatively poorer accuracy was traced to poorer discrimination of tones in the higher frequency ranges. During transfer tests, the discrimination generalized to novel tones when the training tones were included, but not when they were omitted.

Keywords: absolute pitch perception, songbirds

Oscines, the true songbirds, use song as a social signal to defend territory, and male oscines use song to attract females for courtship. How oscines recognize their own species' (conspecifics) songs in acoustic environments crowded with the songs of other species (heterospecifics) has been the subject of much research. It is now well known that songbirds aggregate information from several features (e.g., number of notes, note duration, and trill

notes) to identify conspecifics (Nelson, 1988). However, one acoustic feature, the frequency range of song notes, is cited repeatedly in the literature as important to species recognition. Individual songbirds produce notes within narrowly circumscribed species-typical ranges of spectral frequencies, and birds use this pitch information to help distinguish between conspecific and heterospecific singers. For example, in white-throated sparrows (*Zonotrichia albicollis*), normal songs elicited more territorial defense (e.g., song and approach to the speaker) than song pitch shifted either one octave below or two octaves above the frequencies in normal song (Falls, 1963). Similarly, in field sparrows (*Spizella pusilla*), songs with notes within the normal frequency range elicit more territorial defense than song pitch shifted more than two standard deviations upward (Nelson, 1989b). Moreover, Nelson (1989b) was able to show that sparrows could use frequency simultaneously to identify an individual neighbor and to identify the range of conspecific songs. Interestingly, frequency range is a superordinate feature in song recognition; that is, in field 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, Lemon, & Date, 1986). The finding that frequency range is important to conspecific recognition has been replicated in at least 12 oscine species (e.g., Dabelsteen & Pedersen, 1985; Emlen, 1972; Falls, 1963; Lohr, Weisman, & Nowicki, 1994; Nelson, 1989b; Nowicki, Mitani, Nelson, & Marler, 1989; Thompson, 1969; Weary et al., 1986; Weisman & Ratcliffe, 1989; Wunderle, 1979).

The use of spectral frequency ranges to sort conspecific from heterospecific songs implies that songbirds represent the distribution of pitches in conspecific song notes and use these stored

Tiffany T. Y. Lee, Isabelle Charrier, and Laurie L. Bloomfield, Department of Psychology, University of Alberta, Edmonton, Alberta, Canada; Ronald G. Weisman, Departments of Psychology and Biology, Queen's University, Kingston, Ontario, Canada; Christopher B. Sturdy, Department of Psychology and Centre for Neuroscience, University of Alberta, Edmonton, Alberta, Canada.

Isabelle Charrier is now at the Bioacoustics Team, Université Paris Sud, Orsay, France.

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Correspondence concerning this article should be addressed to Christopher B. Sturdy, Department of Psychology, P217 Biological Sciences Building, University of Alberta, Edmonton, Alberta T6G 2E9, Canada. E-mail: csturdy@ualberta.ca

representations to classify songs and identify conspecifics. In other words, songbirds use absolute pitch (AP) to help them identify conspecific songs. AP refers to the ability to produce, identify, classify, or memorize pitches without the use of a current or recent external reference sound, which is clearly a close fit with what songbirds do when they use frequency range to identify conspecific songs. The purpose of the present research was to coordinate the previously described field studies of song recognition with laboratory operant discrimination procedures to study the accuracy of songbirds' AP.

The study of oscine AP in operant perceptual discriminations originated in Hulse, Cynx, and Humpal's (1984) inadvertent but serendipitous confounding of AP and relative pitch (RP) cues in starlings (*Sturnus vulgaris*). RP refers to the ability to recognize relationships between acoustic frequencies. In training birds in operant discriminations of RP, researchers have presented the same rewarded and unrewarded relative pitch changes on hundreds of trials in note sequences that begin at several different frequencies (e.g., Hulse & Cynx, 1985; Weary & Weisman, 1991; but see MacDougall-Shackleton & Hulse, 1996; Njegovan & Weisman, 1997, for effective alternative procedures for RP testing). If the rewarded tone sequences begin at different frequencies than the unrewarded sequences, then songbirds often learn to discriminate between the sequences using both RP and AP. These studies provide ample evidence that songbirds can sort the starting frequencies of rewarded and unrewarded tones into AP categories. However, as definitive descriptions of AP, studies of confounded RP and AP are of limited value; they can tell us whether animals have AP but not how skillfully animals are using AP.

In the present article, we report on the results of more sensitive and direct tests of oscine AP known as frequency-range discriminations. In frequency-range discriminations, birds learn to classify sine wave tones into ranges on the basis of associations between responses to the tones in successive ranges and reward or nonreward. The task is similar to identifying the frequency ranges of successive notes in conspecific song. In a study that provided a model for the present experiments, Weisman et al. (1998) trained songbirds (zebra finches, *Taeniopygia guttata*) in operant discriminations of 40 tones in the spectral region between 980 Hz and 5660 Hz, spaced 120 Hz apart, and parsed into eight ranges of five tones each (see Table 1). In the S+ first version of the task, responses (hopping or flying to the feeder) to tones in the odd ranges (first, third, fifth, and seventh) were rewarded (with food),

and responses to tones in the even ranges were not rewarded. In the counterbalanced, S- first version of the task, responses to tones in the even ranges were rewarded. In both versions of the task, zebra finches accurately discriminated every shift between reward and nonreward across the eight frequency ranges. In summary, zebra finches can sort tones into eight pitch ranges with high accuracy.

Here we have broadened the study of oscine frequency-range discriminations to include the AP abilities of two closely-related North American songbirds: black-capped chickadees (*Poecile atricapillus*) and mountain chickadees (*Poecile gambeli*). Black-capped chickadees inhabit temperate regions of the northern two-thirds of the United States and much of Canada (Smith, 1993). Mountain chickadees, a closely related species (Gill, Mostrom, & Mack, 1993), prefer alpine regions (McCallum, Grundel & Dahlsten, 1999). In a few geographically unique regions (e.g., areas in the Rocky Mountains), black-capped and mountain chickadees live sympatrically.

Much is known about the songs and calls of black-capped chickadees (see reviews by Hailman, 1989; Hailman & Ficken, 1996; Weisman & Ratcliffe, 2004). In contrast, little is known about the vocalizations of mountain chickadees, except that their whistled songs and buzzy calls are acoustically similar but distinguishable from those of black-capped chickadees (Bloomfield, Charrier, & Sturdy, 2004; Hill & Lein, 1989; Lohr, 1995). Over almost all of their geographical range, male black-capped chickadees sing a two-note vocalization (called the *fee-bee* song) in which the fee and bee notes are separated in pitch by a constant frequency ratio, and individual chickadees transpose the song (holding the ratio constant) across the entire frequency ranges of the fee and bee notes (see Weisman & Ratcliffe, 2004). The songs of mountain chickadees are also composed of clearly whistled notes, but the relationship between the notes, if any, is unknown. However, many mountain chickadee songs begin with a brief introductory note sung at a higher frequency than any note in black-capped chickadee songs, and this brief note is thought to provide a species marker when the two chickadee species live sympatrically (B. Lohr, personal communication, January 3, 2003).

In the current research, we tested zebra finches as well as black-capped and mountain chickadees. We place our studies in two distinct lines of research. In the first line of research, we sought to resolve general questions about AP in oscines. Zebra finches are a colonial species native to arid regions of Australia. By contrast, black-capped and mountain chickadees are a territorial species native to temperate and alpine regions of North America. Research with chickadees provided a test for the generality of precise AP across diverse oscines. Evidence from frequency-range discriminations in zebra finches suggests that AP might be more acute in males than females, but the generality of this sex difference is unknown. Here, we provide evidence from equal numbers of female and male chickadees. Finally, in humans at least, highly accurate AP for musical notes appears to be antithetical to perception of the transposition of RP across a wide range of frequencies (Miyazaki, 1995). It is now well established that black-capped chickadees use RP to transpose their songs (see Weisman & Ratcliffe, 2004, for a review), which suggests that this species might possess less accurate AP than oscine species that rely less on relative pitch.

Table 1
Frequencies (Hz) of S+ (Responses Reinforced) and S- (Responses Unreinforced) Tones in the S- First and S+ First Frequency-Range Discrimination Groups

Frequency range	S- first group	S+ first group	Frequency					
1	S-	S+	980	1,100	1,220	1,340	1,460	
2	S+	S-	1,580	1,700	1,820	1,940	2,060	
3	S-	S+	2,180	2,300	2,420	2,540	2,660	
4	S+	S-	2,780	2,900	3,020	3,140	3,260	
5	S-	S+	3,380	3,500	3,620	3,740	3,860	
6	S+	S-	3,980	4,100	4,220	4,340	4,460	
7	S-	S+	4,580	4,700	4,820	4,940	5,060	
8	S+	S-	5,180	5,300	5,420	5,540	5,660	

In the second line of research, the present experiments serve as preparation for future studies of species differences in chickadees' perception of ecologically valid natural vocalizations. We suspected that these closely-related species, black-capped and mountain chickadees, might be highly similar in AP. Whether different or similar, however, studies of AP provide a baseline for studies of the perception of natural calls and songs. For example, if black-capped and mountain chickadees differed in AP at the specific frequencies found in their natural vocalizations, AP could provide an explanation for species differences in the production and discrimination of notes composed of those frequencies. On the other hand, if the two species had highly similar AP profiles, the similarity would rule out an AP-based explanation of a species difference in the discrimination of notes at those frequencies. More generally, performance in frequency-range discriminations provides baseline control levels of accuracy for future studies of discriminations between the notes in natural vocalizations.

Experiment 1

The purpose of Experiment 1 was to determine the AP abilities of male and female black-capped and mountain chickadees in eight-frequency-range discriminations. Also, we trained a small number of male zebra finches to replicate the precision and low intersubject variability of zebra finches' eight-frequency-range discriminations as demonstrated by Weisman et al. (1998).

Method

Subjects

We trained 32 chickadees—16 black-capped chickadees (*Poecile atricapillus*) and 16 mountain chickadees (*Poecile gambeli*), with equal numbers of males and females in each species—and 4 male zebra finches (*Taeniopygia guttata*). Only a small number of zebra finches were trained because extensive frequency-range data for this species are already available (see Weisman, Njegovan, Williams, Cohen, & Sturdy, 2004). The chickadees were sexed by blood DNA analysis (Griffiths, 2000), and finches were sexed by beak color and plumage (Zann, 1996). None of the birds had prior experience with the stimuli used in these experiments. Chickadees were maintained on a light–dark cycle typical for the season in Edmonton, Alberta, Canada, and zebra finches were maintained on a 12-hr light cycle. We chose these photoperiods on the basis of our extensive experience in maintaining healthy chickadees and zebra finches. Colony room temperatures were maintained at about 20° C. All the birds were treated in accordance with standards set forth by the Canadian Council on Animal Care and the Biological Sciences Animal Welfare and Policy Committee at the University of Alberta.

The chickadees were captured at the Kananaskis field station at Barrier Lake, Alberta, Canada (51° 02'N, 115° 03'W), and the University of Alberta's "Forest Reserve" section of the North Saskatchewan River valley at Edmonton, Alberta, Canada (53°34'N, 113°25' W), under permits and collection licenses from the Environment Canada Canadian Wildlife and Alberta Fish and Wildlife agencies. The chickadees were adults (after 2nd year), as assessed by the shape and coloration of their outer retrices (Pyle, 1997). The zebra finches were obtained as adults from a local supplier.

Chickadees were captured across the year. The number of chickadees available for testing in each season varied with our success in capturing birds. Testing (about 1 month following capture) continued throughout the year, as follows: November–January, 3 black capped, 3 mountain; February–April, 4 black capped, 3 mountain; May–July, 6 black capped, 6 mountain; August–October, 3 black capped, 4 mountain chickadees. We

tested 4 male zebra finches in February–April, at least 1 month following their purchase. Prior to experimentation for a period of 3 to 4 weeks, chickadees were housed individually in visual and auditory but not physical contact with other birds. Housing chickadees in groups in typical indoor aviaries is problematic because of intense intraspecific aggression. Notice that here adult chickadees were housed in visual and auditory contact with other adults. These are not isolate conditions; isolate chickadees are housed away from any contact with adult birds from early in life (see Njegovan & Weisman, 1997; Phillmore, Sturdy, & Weisman, 2003). In fact, the housing conditions in the present research are identical to those for control, non-isolate, field-reared chickadees in previous demonstrations of highly accurate operant discriminations of individual cues (Phillmore et al., 2003) and of RP cues (Njegovan & Weisman, 1997). By contrast, in these same studies, truly isolate-reared chickadees were less accurate at these discriminations. Zebra finches are less aggressive and therefore were safely housed in groups (see Zann, 1996). Species were housed in separate colony rooms. In these details, the housing conditions of chickadees and zebra finches differed: Both chickadees and zebra finches were isolated from conspecifics for 6 to 8 weeks during the experiment, whereas chickadees but not zebra finches were prevented from conspecific contact for 3 or 4 weeks. It is important to know that chickadees normally separate from conspecifics while establishing territories prior to the breeding season. We view the difference between species as an unavoidable consequence of comparing species, similar to the difference in the food rewards made available to chickadees and zebra finches. We would be surprised if the difference in housing or in food rewards accounted for the difference we will describe here. Moreover, we are uncertain how one could determine whether these differences are important to the comparative psychology of AP. After all, one cannot feed simple grain to chickadees or house them together without damaging the birds and thus invalidating the experiments.

Chickadees and zebra finches, respectively, had free access to Mazuri small bird maintenance food (Purina Mills LLC, St. Louis, MO) or Hagen Finch Mix (Rolf C. Hagen Canada, Montreal, Quebec, Canada). All birds had free access to grit, cuttle bone, and water. On alternative days (6 days weekly), the birds had access to a single mealworm (chickadees) or small amounts of hard-boiled egg mixed with spinach (zebra finches). All birds had a vitamin supplement (Hagen Vitamin Conditioner for Birds, Montreal, Quebec, Canada) added to their water.

During training, the food provided prior to experimentation was available but only as reward during visits to the automated feeder. Access to food supplements, grit, cuttle bone, and water (with vitamin supplements) continued as before training. Chickadees and zebra finches were weighed once a week; they never fell below 90% of their free-feeding weights. Clearly, our procedures were effective in ensuring adequate food motivation and in maintaining small birds in good health (e.g., Weisman et al., 1998; Phillmore et al., 2003). To further ensure that the birds maintained good general health, the authors and the animal care staff observed them daily.

Apparatus

Birds were housed individually in modified budgerigar cages (0.3 m wide × 0.4 m high × 0.4 m deep) for 6 to 8 weeks during experimentation. To ensure that the birds could not eat spilled food, we attached a mesh floor to the bottom of the cage. An opening (11 cm × 16 cm) in the cage allowed access to an automated feeder. Cages had several perches and dispensers for water and grit. Each cage was housed in a ventilated, sound-attenuating chamber illuminated by a 9-W twin-tube, full-spectrum fluorescent bulb. Infrared cells monitored the bird's position at the feeder (Njegovan, Hillhorst, Ferguson, & Weisman, 1994) or at a perch directly opposite the feeder. A single-board computer (Palya & Walter, 2001) interfaced to a personal computer controlled a standard CD-ROM, scheduled the experiment, and recorded responses to stimuli. Tone stimuli were played from a CD to either a Cambridge A300 Integrated Amplifier (Cambridge Audio,

London, England) or a NAD 310 Integrated Amplifier (NAD Electronics, London, England) and then to a Fostex FE108 full-range speaker (Fostex, Japan) located beside the feeder. The center of the speaker was at the height of the bird's head when the bird stood on the perch. Calibration of tone stimuli in the operant chambers was performed, and periodically retested, with an Integrating Sound Level Meter Type 2239A (Brüel & Kjær Canada, Point Claire, Quebec, Canada).

Stimuli

Pure sine wave tone stimuli, 440 ms in duration, were synthesized with SIGNAL 4.0 for Windows (Engineering Design, Belmont, MA), 44,100 16-bit samples per second. Each tone was ramped at onset and offset for 5 ms to avoid transients. Forty tones were synthesized from 980 to 5660 Hz, at 120-Hz intervals (Table 1). It is well understood that discrimination of the pitch of a tone is not independent of its amplitude (see Moore's, 1989, authoritative book on hearing, p. 162). That is, depending on the spectral frequency of a tone, the louder of two renditions will be perceived as either higher or lower in pitch. The effect is usually small but the relationship between loudness and perceived pitch is complex, nonlinear, and poorly understood. However, Moore (1989) and Emmerich, Ellermeier, & Butensky (1989) note that playing a tone at more than one amplitude slightly increases the variability of pitch discrimination by unconfounding pitch from amplitude judgments. Here, we reduced the dependency of pitch discrimination on tone amplitude by playing each tone at two amplitudes, either 70 dB or 80 dB at random from tone to tone across sessions. Notice that this counterbalancing approach makes frequency a more salient determinant of pitch discrimination by eliminating the possibility of confounding with amplitude. Also, notice that the procedure controls for amplitude without providing the extensive data necessary to study the interaction with pitch. This is hardly surprising as the interaction was not the subject of our research.

Procedure

Nondifferential training. Once birds learned to use the perch and feeder (usually in about 3 weeks), nondifferential training began. We used nondifferential training to create a high and uniform baseline percentage of responses across training tones from which to assess the effects of subsequent discrimination. To initiate a trial, birds had to remain on a request perch, directly across from the feeder, for a randomly selected time interval between 900 and 1,100 ms. Following this interval, a tone was randomly selected without replacement and played. If the bird flew or hopped to the feeder, the trial ended with 1-s access to food followed by a 30-s intertrial interval. If the bird left the perch but did not enter the feeder, the trial ended after 1 s. If the bird remained on the perch, the trial ended after 1 s and a 60-s intertrial interval followed. If the bird left the perch before the tone finished playing (i.e., did not listen to the entire tone), the sequence ended, the chamber light was darkened for a 30-s intertrial interval, and the sequence was not included in the total number of trials. These procedures ensured that birds left the perch on each trial and did so after hearing the tone in its entirety. Nondifferential training continued until birds responded to all tones about equally and on at least 60% of the trials. Once the birds responded to all the tones at a high and consistent level (about 3,000 trials, or 3 days), discrimination training began.

Discrimination training. The stimulus set of 40 tones was separated into eight 5-tone ranges (i.e., 5 contiguous tones per range). Birds were assigned to one of two counterbalanced discrimination groups, S+ first or S- first (see Table 1). The S+ first group received food for responding to tones in the first, third, fifth, and seventh ranges of five stimuli each. The S- first group received food for responding to tones in the second, fourth, sixth, and eighth ranges. If the bird visited the feeder after a rewarded (S+) tone (see Table 1), the trial ended with 1-s access to food followed by a 30-s intertrial interval. If the bird visited the feeder after an unrewarded

(S-) tone (see Table 1), the trial ended without food presentation and the chamber light was darkened for a 30-s intertrial interval. All other procedures were the same as during nondifferential training.

The discrimination criterion was a discrimination ratio of ≥ 0.80 for 3,000 consecutive trials (roughly 3 days) or a maximum of 15,000 trials, whichever was achieved first. This criterion was used in prior frequency-range discriminations (e.g., Weisman et al., 1998), and the maximum number of trials was chosen to provide chickadees with an increased opportunity to acquire accuracy at the task.

Response Measures and Statistical Analyses

We calculated the percentage of responses to each tone by dividing the number of feeder visits by the number of trials for that tone and multiplying by 100. We then calculated the discrimination ratio by dividing the average percentage of responses to tones in the S+ frequency ranges by the average percentage of responses to tones in the S+ and S- frequency ranges. We also recorded the number of trials to the 0.80 criterion; birds that never met the discrimination criterion were assigned the maximum of 15,000 trials.

We conducted analyses of variance (ANOVAs) on the response measures. The percentage of response and discrimination ratio measures may not be normally distributed when sample percentages and ratios are near 0% and 100%, or 0.5 and 1.0, respectively. Trials to criterion may not have been normally distributed when several birds in each group failed to meet criterion in the allotted number of trials. We conducted parallel ANOVAs of the square root arcsine transform of the percentage response and discrimination ratio measures and a square root transform of trials to criterion. We also conducted parallel ANOVAs using rank scores for each measure (Conover & Iman, 1981). Analysis of the transformed data yielded virtually the same levels of significance as analysis of the untransformed scores; we report the untransformed data below.

Results and Discussion

The purpose of our analysis was to determine whether zebra finches and chickadees, and among chickadees, black-capped and mountain chickadee males and females, differed in speed of acquisition (trials to criterion) or in final performance (discrimination ratio in the final 1,000 trials) in the frequency-range discrimination. Also, we examined differences between species in their percentages of response to the 40 tones in the S+ and S- first orders of the frequency-range discrimination.

Trials to Criterion

Figure 1 shows mean trials to criterion for male zebra finches and male and female black-capped and mountain chickadees. In a between-subjects ANOVA conducted with data from male birds only, we found a significant main effect for species, $F(2, 14) = 9.39, p = .003$, but no significant main effect between the S+ and S- first discrimination tasks, $F(1, 14) = 0.02, p = .89$, or interaction with discrimination tasks, $F(2, 14) = 1.27, p = .31$. The S+ and S- first discriminations were acquired in highly similar numbers of trials ($M \pm 95\%$ confidence interval [CI]): the S+ first task = $13,500 \pm 1,634$ and the S- first task = $13,600 \pm 1,687$. Tukey's honest significant difference (HSD) tests ($p \leq .05$) showed that zebra finch males acquired the frequency-range discrimination in significantly fewer trials than either black-capped or mountain chickadee males, which did not differ significantly in trials to criterion. We excluded zebra finches and focused on comparisons between chickadee species in a between-subjects ANOVA but observed no significant main effects for

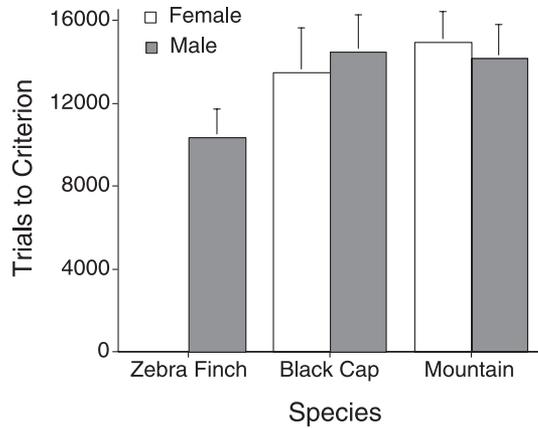


Figure 1. Results in the S+ first and S− first tasks are averaged to show mean trials to criterion in the eight-range discrimination for male zebra finches and male and female black-capped and mountain chickadees. Error bars show the 95% confidence interval.

discrimination task, species, or sex, $F_s(1, 24) \leq 0.67$, $p \geq .42$, and no significant interactions between the main effects, $F_s(1, 24) \leq 1.87$, $p \geq .18$. In summary, the main finding was that zebra finches acquired the frequency-range discrimination in fewer trials than did either chickadee species.

Discrimination Ratios

Figure 2 shows discrimination ratios in the final 1,000 trials for male zebra finches and male and female black-capped and mountain chickadees. In a between-subjects ANOVA conducted with data from male birds only, we found a significant main effect for species, $F(2, 14) = 5.75$, $p = .015$, but no significant effect for discrimination task, $F(1, 14) = 0.01$, $p = .76$, or interaction with discrimination tasks, $F(2, 14) = 1.16$, $p = .34$. Discrimination ratios in the S+ and S− first tasks were highly similar ($M \pm 95\%$ CI): $.82 \pm .04$ and $.80 \pm .06$, respectively. Simple effects and Tukey HSD tests ($ps < .05$) showed that zebra finch males acquired a more accurate frequency-range discrimination than either black-capped or mountain chickadee males, which did not differ significantly in accuracy. We excluded zebra finches and focused on comparisons between chickadee species in a between-subjects ANOVA but observed no significant main effects for discrimination task, species, or sex, $F_s(1, 24) \leq 0.97$, $p \geq .33$, and no significant interactions between the main effects, $F_s(1, 24) \leq 0.16$, $p \geq .69$. Differences between male and female chickadees in acquisition and final discrimination ratios were small, inconsistent, and nonsignificant. In summary, the main finding was that zebra finches attained higher discrimination ratios (better accuracy) in the frequency-range discrimination than either chickadee species.

Percentage of Response Across Frequency Ranges

Analysis of discrimination ratios found that all three species accurately sorted the tones into frequency ranges, but zebra finches were more accurate than chickadees. We determined the source of these differences by comparing species in the percentages of response to tones in the four S+ and four S− ranges. Figure 3

shows percentages of response separately by species for the S+ first and S− first tasks.

In separate repeated measures ANOVAs, we found no statistically significant differences in the percentage of responses male and female black-capped and mountain chickadees allocated to tones in the S+ and S− ranges in the S+ first and S− first tasks ($F_s < 1$). In subsequent analyses, we compared chickadees (males and females of both species) with zebra finches. As shown in Figure 3, chickadees discriminated between S+ and S− tones in the higher frequency ranges less accurately than zebra finches, but less accurate discrimination at higher frequencies in chickadees took a different form in the S+ first and S− first tasks. To provide tractable statistical analyses of these effects, we averaged percentages of response over the five tones in each range. In these analyses, a comparison between the S+ first and S− first tasks is called a task-order effect. In separate repeated measures ANOVAs of S+ and S− responding, we found significant interactions between task order, species, and frequency ranges, $F_s(3, 48) \geq 3.34$, $ps \leq .03$. Analyses of simple effects ($p < .05$) revealed that (a) in the S+ first task, the percentage of S+ response declined progressively from the lowest to the highest frequency range in chickadees but not in zebra finches and (b) in the S− first task, the percentage of S+ response did not differ significantly across ranges or species. The opposite pattern was observed for S− responding: (a) in the S+ first task, the percentage of S− response did not differ significantly across ranges or species and (b) in the S− first task, the percentage of S− response increased progressively from the lowest to the highest frequency range in chickadees but not in zebra finches. In summary, the main finding was that the lower discrimination ratios of chickadees than zebra finches in eight-frequency-range tasks were traced to chickadees' less accurate discrimination among tones in the higher frequency ranges (see Figure 3).

Tests for Seasonal Variation

Cynx and Nottebohm (1992) found that zebra finches learned operant discriminations between conspecific vocalizations more

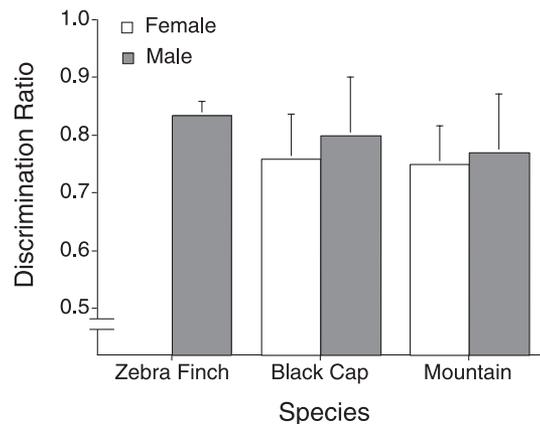


Figure 2. Results in the S+ first and S− first tasks are averaged to show mean discrimination ratios in the eight-range discrimination for male zebra finches and male and female black-capped and mountain chickadees. The discrimination ratio was .5 when performance in the task was at chance. Error bars show the 95% confidence interval.

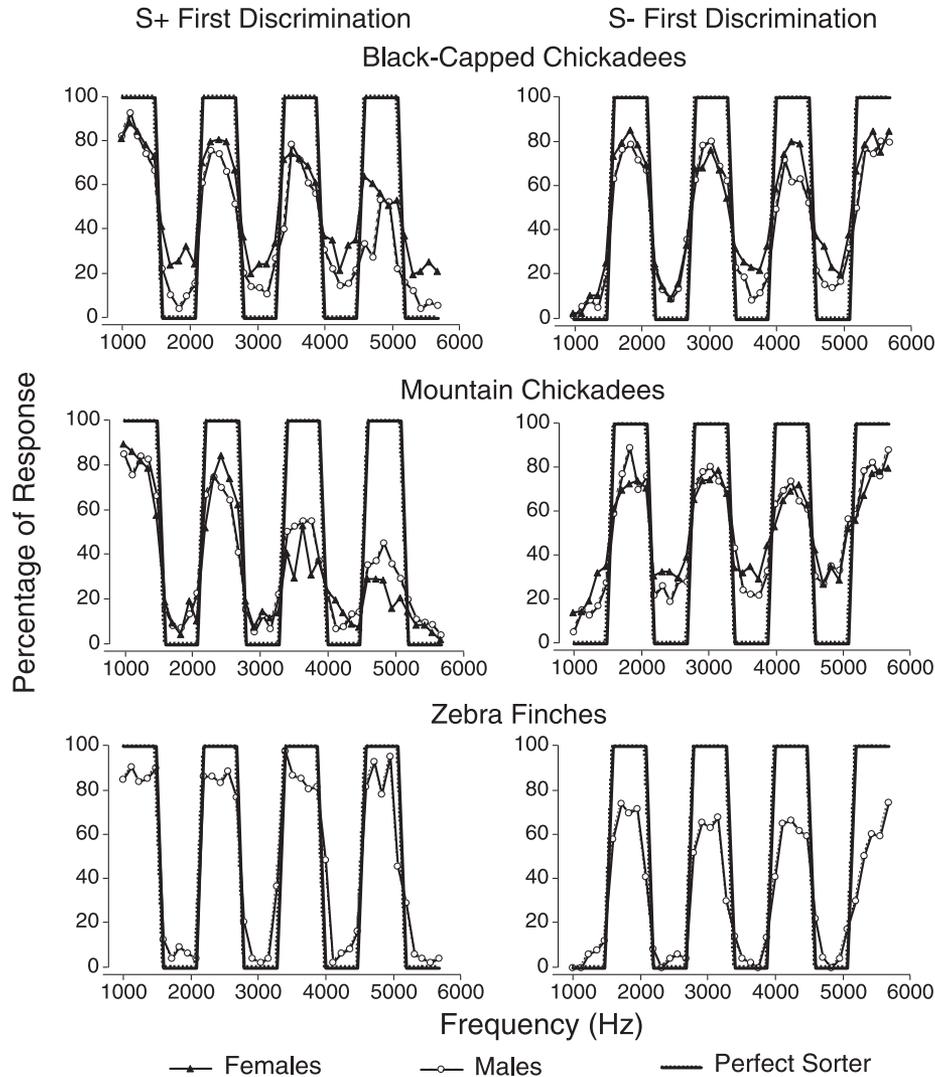


Figure 3. Mean percentage of responses for male and female black-capped and mountain chickadees and male zebra finches in the S+ first and S- first counterbalancing of the eight-range discrimination. The dashed lines show performance of a perfect sorter: responding at 100% to all S+ tones (rewarded stimuli) and at 0% to all S- tones (unrewarded stimuli).

rapidly in summer than in winter. This led us to ask whether the species differences between zebra finches and chickadees we have already reported hold for birds tested in the same season. We compared zebra finches with chickadees trained in the eight-range frequency discrimination in the same season (February–April) in between-subjects ANOVAs conducted separately for trials to criterion, $F(2, 8) = 71.93, p = .0001$, and discrimination ratios, $F(2, 8) = 7.30, p = .016$; both ANOVAs yielded significant main effects for species tested in the same season. Tukey HSD tests ($ps \leq .05$) found that zebra finches acquired the discrimination in fewer trials and to a higher standard (discrimination ratio) than black-capped and mountain chickadees, which did not differ. The means and standard errors for samples of chickadees tested February–April were virtually identical to those already reported for the whole group tested across the year (see Figures 1 and 2). This finding, in turn, led us to ask whether chickadees tested in

different seasons differed in the frequency-range discrimination. In between-subjects ANOVAs conducted separately for trials to criterion and discrimination ratios, respectively, we found no significant main effects for season, $Fs(3, 24) \leq 1.71, ps \geq .19$, species, $Fs(1, 24) \leq .29, ps \geq .59$, or their interaction, $Fs(3, 24) \leq 1.62, ps \geq .21$. In an interesting example of these nonsignificant effects, chickadees trained during the shortest days of the year, November–January, learned in fewer trials ($M \pm 95\% \text{ CI} = 12,833 \pm 3362$) and to a higher standard discrimination ratio ($.76 \pm .10$) than birds trained during the longest days, May–July (trials, $14,250 \pm 1544$; discrimination ratio, $.71 \pm .07$). In other words, the effects of season on the discrimination of frequency ranges of sine wave tones in chickadees were in the opposite direction from those reported for discriminations of conspecific vocalizations in zebra finches and, in any event, were not statistically significant. Also, and most important here, our conclusion that zebra finches are

superior to chickadees in classifying tones into frequency ranges holds for zebra finches and chickadees tested in the same season of the year.

Experiment 2

Transfer from training to novel stimuli is a hallmark of effective categorization. As a further test of frequency-range categorization in chickadees and zebra finches, we examined transfer (generalization) to novel tones from the same eight-frequency-range categories as the training stimuli used in Experiment 1. The experiment paralleled the transfer test Njegovan, Ito, Mewhort, and Weisman (1995) conducted with zebra finches in a three-frequency-range discrimination. Njegovan et al. (1995) interspersed novel tones with training tones during the transfer test and found excellent transfer to the novel tones. In Experiment 2, we examined two transfer procedures. Initially, we presented novel tones only (omitting the training tones) during the transfer test, but the birds responded much more to novel tones in the S- frequency ranges than they had to training tones in the S- frequency ranges. We then adopted Njegovan et al.'s (1995) procedure for the remaining birds: presenting novel tones interspersed among training tones during a probe test. In Experiment 2, we report on transfer to novel tones presented in the context of the training stimuli (the probe test) and without the context of the training stimuli (the novel tones only test).

Method

Subjects and Apparatus

The animals and apparatus were the same as in Experiment 1, except that 3 birds (1 black-capped chickadee and 2 mountain chickadees) were discontinued from experimentation because of illness during the period between training in Experiment 1 and transfer testing in Experiment 2.

Stimuli

Thirty-two novel pure sine wave tones were synthesized with the same criteria as the 40 training tones used in Experiment 1. The novel tones (see Table 2) were displaced upwards in frequency by 60 Hz from adjacent training tones, except that novel tones falling at the boundaries between frequency ranges were omitted (compare Tables 1 and 2), because responding to these tones was likely to be intermediate and thus uninformative about whether the discrimination generalized to novel tones. The novel

tones, like the training tones, were each synthesized at 70 dB and 80 dB (sound pressure level). Hence, we presented 64 novel tones in all; the 32 tones shown in Table 2 played at 70 dB and 80 dB. The training tones used in the probe test were the same as those used in Experiment 1 (see Table 1).

Procedure

In the novel tones only group, during a single session we presented the 64 novel tones once each in random order without replacement, but the training tones were omitted. Responses to the novel tones were always rewarded. This group included 4 black-capped and 3 mountain chickadees.

In the probe group, we alternated training sessions with test sessions for eight sessions: four training and four test sessions. Training sessions were as in Experiment 1. During each test session, we presented the training tones (see Table 1) each 10 times and 16 of the novel tones once each in random order without replacement interspersed among the training tones. Over the test sessions, we presented all 64 novel tones (i.e., 16 of the tones shown in Table 2 per session \times 4 sessions). Responses to the training tones were assigned the same trial outcomes as in Experiment 1, but responses to the novel tones were always rewarded. This group included 11 black-capped chickadees, 11 mountain chickadees, and 4 zebra finches.

Response Measures and Statistical Analyses

Discrimination ratios were calculated as in Experiment 1 but separately for training and novel tones. Also, we averaged the percentages of response separately over training and novel tones in the S+ frequency ranges for each subject. In the novel tones only group, discrimination ratios and percentages of response for the training tones were obtained from a training session just prior to the test. In the probe group, discrimination ratios and percentages of response for the training tones were obtained from interspersed presentations of training and novel stimuli during the same test sessions. As in Experiment 1, we conducted parallel ANOVAs of untransformed and transformed discrimination ratios and percentages of response; the levels of significance were similar, so we report our analyses of the untransformed data.

Results and Discussion

The purpose of our analysis was to determine whether male and female black-capped and mountain chickadees and male zebra finches sorted novel tones into the same frequency-range categories as the training tones. We used discrimination ratios and average percentages of response to tones in the S+ frequency ranges to compare performance between the training and novel tones.

Discrimination Ratios

Figure 4 shows that chickadees' discrimination ratios fell to near .5 (chance) during transfer in the novel tones only group but remained at the level of the training discrimination ratio in the probe test group. In one-sample *t* tests, the novel tones discrimination ratio was significantly above chance in both the novel tones only group, $t(6) = 2.87$, $p = .035$, and the probe test, $t(21) = 15.57$, $p = .0001$. However, 2 birds in the novel tones only group had transfer ratios of .5, and the ratios of other birds were near .5, whereas in the probe group all the birds had transfer ratios $\geq .7$.

A repeated-measures ANOVA found a significant interaction between transfer test groups (novel tones only test vs. probe test) and stimuli (training vs. test tones), $F(1, 24) = 87.71$, $p < .0001$, but no significant main effect for species or significant interactions

Table 2
Frequencies (Hz) of Novel Transfer S+ (Responses Reinforced) and S- (Responses Unreinforced) Frequency Range Tones in the S- and S+ First Discrimination Groups

Frequency range	S- first group	S+ first group	Frequency			
1	S-	S+	1,040	1,160	1,280	1,400
2	S+	S-	1,640	1,760	1,880	2,000
3	S-	S+	2,240	2,360	2,480	2,600
4	S+	S-	2,840	2,960	3,080	3,200
5	S-	S+	3,440	3,560	3,680	3,800
6	S+	S-	4,040	4,160	4,280	4,400
7	S-	S+	4,640	4,760	4,880	5,000
8	S+	S-	5,240	5,360	5,480	5,600

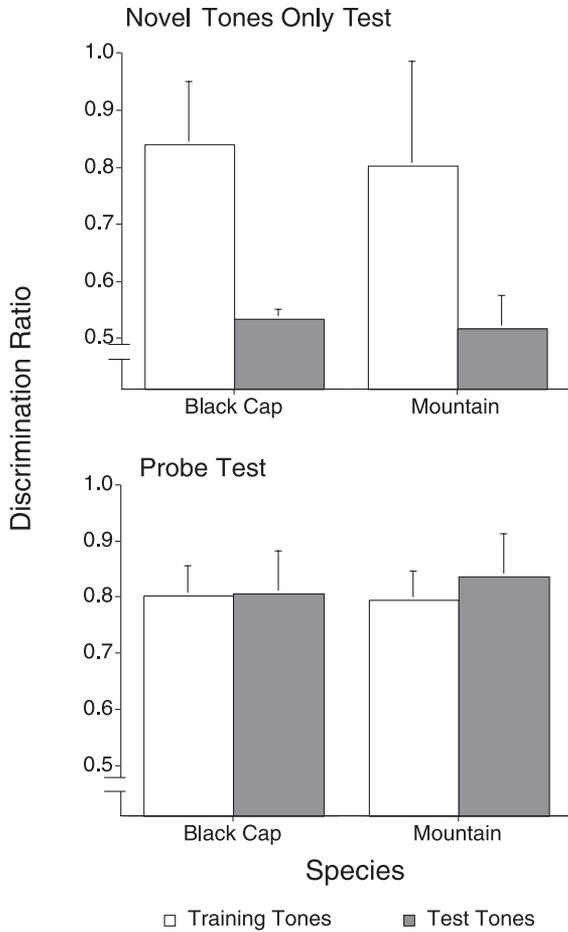


Figure 4. Results in the S+ first and S- first tasks for males and females are averaged to show mean discrimination ratios for the novel and training tones (error bars show 95% confidence intervals) for black-capped and mountain chickadees in the novel tones only and probe test groups. The discrimination ratio was .5 when performance in the task was at chance. The probe test included both training and novel tones, and the novel tones only excluded the training tones.

with species, $F_s(1, 24) \leq .58, p_s \geq .45$. In tests of simple effects ($p < .05$), transfer discrimination ratios were significantly lower than training ratios in the novel tones only group but not in the probe group. Separate ANOVAs found no significant effects for task order (S+ vs. S- first tasks) or sex (females vs. males), $F_s(1, 24) \leq 1.59, p_s \geq .20$. Results for zebra finches are available only from the probe test, where mean discrimination ratios were identical for training tones ($M \pm 95\% \text{ CI} = .88 \pm .04$) and novel tones ($.88 \pm .07$). In summary, the main finding was that when the training tones were available during the probe test, transfer to the novel tones was virtually perfect, but when the training tones were unavailable during the novel tones only test, transfer of the discrimination was statistically significant but very weak.

Percentages of Response to S+ Range Tones

We examined the percentages of response measure to determine whether the novel tones only test affected discrimination ratios by

reducing responding to novel tones in the S+ ranges. Figure 5 shows that the mean percentage of response remained unchanged between training and novel tones, at about 60%, in black-capped and mountain chickadees. A repeated-measures ANOVA found no significant main effects or significant interactions, $F_s(1, 24) \leq .61, p_s \geq .44$. Separate ANOVAs found no significant effects for task order (S+ vs. S- first tasks) or sex (females vs. males), $F_s(1, 24) \leq 1.06, p_s \geq .29$. Results for zebra finches are available only from the probe test, where the mean percentages of response to novel and training tones in the S+ ranges were nearly identical ($M \pm 95\% \text{ CI} = 84.4 \pm 8.9$ and 85.0 ± 8.5 , respectively). In summary, the main finding was that the probe transfer test did not appear to disrupt responding to training or novel tones in the S+ ranges.

General Discussion

Zebra finches acquired the eight-frequency-range discrimination more rapidly and to a higher standard of accuracy than either

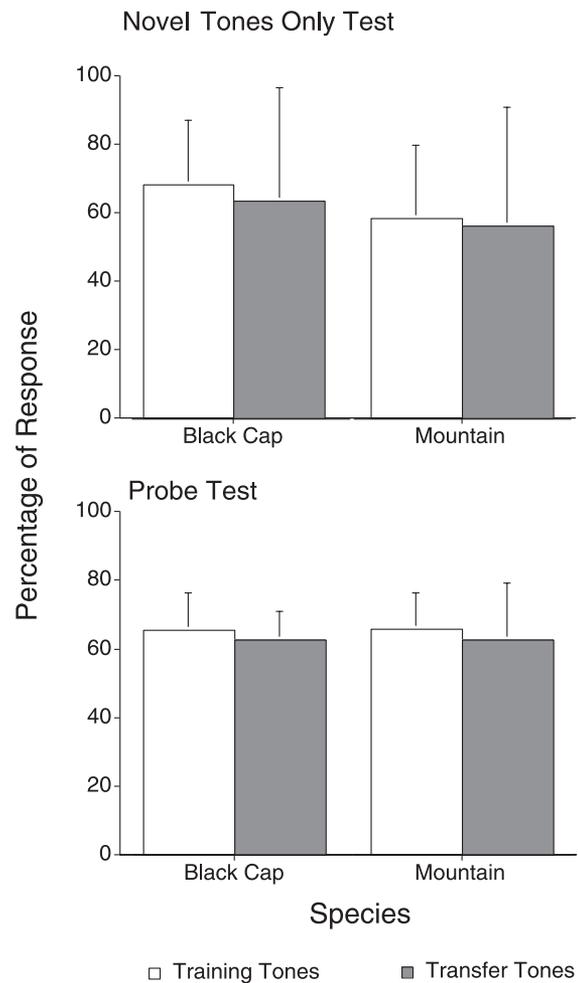


Figure 5. Results in the S+ first and S- first tasks for males and females are averaged to show mean percentage of response to novel and training tones in the S+ frequency ranges (error bars show 95% confidence intervals) for black-capped and mountain chickadees in the novel tones only and probe test groups. The probe test included both training and novel tones, and the novel tones only excluded the training tones.

black-capped or mountain chickadees, which did not differ appreciably in either acquisition or final discrimination. Chickadees' relatively poorer performance can be traced to a subtle difference between zebra finches and chickadees in their discrimination of tones in the higher frequency ranges. Zebra finches sorted S+ and S- tones into ranges with about the same accuracy independent of spectral frequency in both the S+ first and S- first frequency-range tasks. That is, zebra finches responded at a high and consistent level to S+ tones and at a low and consistent level to S- tones in each spectral range in both counterbalancings of the task. In contrast, in the S+ first task, chickadees responded less to higher than to lower frequency S+ tones, and in the S- first task, chickadees responded more to higher than to lower frequency S- tones.

The frequency-range discriminations of male and female chickadees of both species were remarkably similar: Male and female chickadees acquired the discrimination in similar numbers of trials and to about the same standard. Furthermore, both sexes showed the same pattern of reduced sensitivity in discriminating tones at higher frequencies in the S+ and S- first tasks.

Transfer tests of generalization of the frequency-range discrimination to novel tones had opposite effects depending on whether the training tones were included in the test. When the training tones were included (the probe test), chickadees accurately sorted novel tones into the same frequency ranges as the training tones. When the training tones were excluded (the novel tones only test), chickadees sorted the tones into ranges only marginally better than chance.

The Logic of Cross-Species Comparisons of Perceptual Ability

We conducted the present research to explore how auditory perception has evolved in songbirds and, in particular, whether different species have evolved specializations in AP. As one might expect, caution is necessary in comparisons among species because of differences in responsiveness, motivation, and a host of other factors. However, a comparative psychology of audition on the basis of rote similarity between the responses and motivation used in contrasts among species is probably impossible and, in any case, would hardly be worth the effort. Here, we propose another standard for assessing perceptual control across variables that change from species to species in comparative research. This is an adaptation of the use of positive controls that has been applied with much success in behavioral neuropharmacology to establish a standard expected drug action (e.g., Sanchez, Gruca, Bien, & Papp, 2003).

In the context of comparative studies of perception, positive controls can be used to establish the validity of a testing procedure. For example, the general discrimination methodology used here has been effective in demonstrating that chickadees and zebra finches can accurately discriminate the relative pitch of sequences of tones (Njegovan & Weisman, 1997; Weisman, Njegovan, & Ito, 1994) and that both species discriminate accurately among conspecific vocalizations (Sturdy, Phillmore, Price, & Weisman, 1999; Sturdy, Phillmore, & Weisman, 2000). The argument here is unambiguous (see also Weisman et al., 1998, 2004): If a methodology is effective in producing highly accurate discriminations of a number of auditory attributes in a given species, then lesser

accuracy with another auditory attribute is unlikely to be the result of failure in the already established methodology but more likely reflects a true perceptual deficiency in the species under test.

Species and Sex Differences in Frequency-Range Discriminations

It is important to put differences in AP among oscines in comparative perspective. In frequency-range tasks virtually identical to those described here, humans and rats sorted tones only slightly better than chance, that is, with discrimination ratios just above .5 (Weisman et al., 1998, 2004). In contrast, in the present study, zebra finches, black-capped chickadees, and mountain chickadees sorted tones much more accurately than either humans or rats, with discrimination ratios of .83, .78, and .76, respectively. In a comparative perspective, then, although chickadees and zebra finches differed in accuracy, all our oscine study species had good AP in the eight-frequency-range task.

Differences in the accuracy of AP between male zebra finches and male and female chickadees observed in the present research led us to compare our results in more detail with those of previous studies of oscines in the eight-range discrimination task (Weisman et al., 2004). Figure 6 shows the eight-range S+ first discriminations of male ($n = 7$) and female zebra finches ($n = 6$) and female white-throated sparrows ($n = 6$), redrawn from Weisman et al. (2004). The results for male zebra finches are virtually identical to those reported here: highly accurate discrimination of every frequency range. This replication is not surprising, but it is important methodologically because the two studies were conducted in different laboratories, and we improved on Weisman et al.'s (1998) digital signals. They used 8-bit 22.05-kHz tones and we presented 16-bit 44.1-kHz tones. Most important, female white-throated sparrows responded less to higher than lower frequency S+ tones, a pattern of responding similar to that observed in male and female

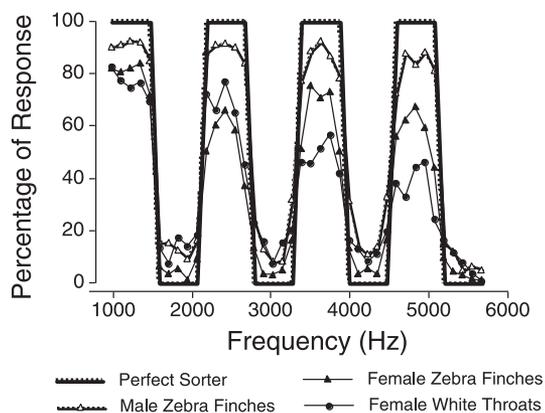


Figure 6. Mean percentage of responses for male and female zebra finches and female white-throated sparrows in the S+ first counterbalancing of the eight-range discrimination. The dashed lines show performance of a perfect sorter: responding at 100% to all S+ tones (rewarded stimuli) and at 0% to all S- tones (unrewarded stimuli). Redrawn from "A Behavior Analysis of Absolute Pitch: Sex, Experience, and Species" by R. G. Weisman, M. G. Njegovan, M. T. Williams, J. S. Cohen, and C. B. Sturdy, 2004, *Behavioural Processes*, 66, p. 299, with permission. Copyright 2004 by Elsevier B. V.

chickadees in the present study. Female zebra finches were intermediate between male zebra finches and female white-throated sparrows: They showed only slightly reduced responding to higher frequency S+ tones.

On the basis of the results shown in Figure 6, Weisman et al. (2004) suggested that female songbirds might be generally less accurate than males (i.e., might be sexually dimorphic) in their ability to sort pitches into ranges. In the present research, the frequency-range discriminations of male and female chickadees were highly similar (i.e., not dimorphic) and were also similar to those of female white-throated sparrows (reported by Weisman et al., 2004; see Figure 6). In chickadees and white-throated sparrows, discrimination between S+ and S− tones was less accurate at the higher frequency ranges than in male zebra finches. On a continuum, the frequency-range discrimination of female zebra finches was more similar to that of male zebra finches than to the discriminations of the other oscines tested so far. Furthermore, the evidence suggests that differences in AP between male and female conspecifics might vary from slight to insubstantial. Taken together, Weisman et al.'s (2004) and our results suggest a continuum of high quality AP among oscine species, with differences along the continuum resulting mainly from errors in sorting higher frequency tones in the frequency-range discriminations.

We have described changes in responding in chickadees at higher frequencies in the S+ and S− first tasks and even used them as markers of similar AP between males and females and of differences in AP between chickadees and zebra finches. One might suggest an explanation based strictly on a performance deficit in chickadees, namely, that higher frequency sine wave tones resemble chickadee alarm calls (see Ficken, Ficken, & Witkin, 1978) and therefore might cause chickadees to be wary of approaching the speaker and feeder after their presentation. However, this performance-based explanation fails to provide a principled explanation of our results. In the S+ first task, chickadees do approach the feeder less after higher frequency tones, but in the S− first task, they approach the feeder as often after higher as lower frequency tones. If chickadees are wary of high frequency tones, why do they then approach higher frequency tones in the S− first task?

The finding of opposite trends in responding in the S+ first and S− first tasks led us to reject a performance-based explanation and turn to an explanation based on the perceptual competence of chickadees to explain performance in both the S+ first and S− first tasks. A general, competence-based explanation follows. Accurate performance in frequency-range discriminations requires resolution of the pitches in tones, memory for those pitches, and representation of the contingencies between the tones and reward. Weisman et al. (1998) included all three in their neural network model for performance in frequency-range discriminations. Briefly, Weisman et al. (1998; see also Shepard & Kannappan, 1991) accounted for the discrimination using a network of auditory filters (in neural terms, a tonotopic pitch map) with connections to a representation of trial outcome (reward and nonreward). According to Weisman et al.'s (1998) model, performance is a function of the spread of sensory excitation produced by a tone across auditory filters in the map (the AP component) and associations between those sensory filters and the trial outcome unit. In the language of signal detection theory (see Killeen, 1992; Nevin, 1969, for reviews), biases can occur in frequency-

range discriminations when the spread of excitation across auditory filters interacts with associations between the filters and the trial outcome unit, and these biases can influence performance in frequency-range discriminations.

When the tones produce only limited spread between sensory filters, as is likely in zebra finches, birds are rarely uncertain about which tone was presented, the effect of biases inherent in the task are therefore slight, and accuracy is high across spectral frequencies. When tones produce greater sensory spread between filters, as is likely at higher frequencies in black-capped and mountain chickadees and white-throated sparrows, birds are more uncertain about which of the higher frequency tones was presented, the effect of sensory and outcome asymmetries is therefore greater, and accuracy varies with spectral frequency in accordance with biases inherent in the S+ and S− first tasks.

In summary, the sensory representation of stimuli and discrimination biases (inherent in any correlation between stimuli and response outcomes) jointly determined the pattern of responding in our discrimination tasks. Because we counterbalanced the correlations between tones and outcomes in the S+ first and S− first tasks, we were able to disentangle the differential effects of pitch sensitivity and response outcome in chickadees' frequency-range discriminations and verify the reduced discrimination of tones in the higher frequency ranges in both tasks.

Transfer of Frequency-Range Discriminations to Novel Tones

Territorial neighbors, mates, and nearby heterospecific birds are sometimes lost through attrition and replaced over a breeding season and from year to year. In order for songbirds to use the frequency ranges of the notes in song effectively, they must generalize their discrimination of conspecific songs widely over familiar and novel song notes. In Experiment 2, we tested whether the transfer of frequency-range discriminations to novel tones can provide a model for how oscines might use AP for frequency ranges to sort conspecifics from heterospecifics, neighbors from strangers, and mates from other males in a changing mix of song frequencies.

We observed near perfect transfer to novel tones when the training tones were included and provided context for the discrimination (in the probe test), but we observed at best slight evidence of transfer when the training tones were excluded (in the novel tones only test). Oscines are most likely to hear the songs of unfamiliar birds in the context of the songs of familiar birds because it is unlikely that over a season or even across years all the familiar birds will have been lost or strayed from the area. Thus, the probe test provides the best evidence that birds are likely to transfer their knowledge about the frequency ranges of conspecific song notes from the songs of familiar to unfamiliar birds.

We hoped that a test with novel tones alone might provide rapid and clear evidence of transfer. In one sense, it did: The birds responded about as much to novel as to training S+ range tones. But in a more important sense, it did not: The birds failed to discriminate (i.e., respond less to) novel tones in the S− frequency ranges. We uncovered this context-induced transfer failure quite accidentally. However, the failure was instructive. Despite similarities between the novel and training tones (they were separated by only 60 Hz), the birds detected the omission of the training

tones from the novel tones only test. It appears that inclusion of the training tones provided a context for successful transfer to the novel tones in the probe test.

Context change is a well-known determinant of retrieval failure (see Blough, 1998; Bouten, Nelson, & Rosas, 1999, for reviews). Here, the context of the training tones and their response outcomes was clearly important to retrieval of the frequency-range discrimination for transfer to novel tones, whereas omission of the context of the training tones and their response outcomes from a transfer test led to a nearly complete loss of the discrimination of frequency ranges. Further research to explore the conditions that induce transfer success and failure is suggested. For example, do the training tones themselves provide context for generalization of the discrimination to novel tones, or do the training response outcomes contribute importantly to the context? Also, one wonders whether any stimuli, context specific or not, might enhance discrimination in the probe group? Against this idea, Bouten et al. (1999) have shown that to enhance retrieval, stimuli must be part of the training context, but irrelevant sounds could be presented during probe tests in future research.

Frequency-Range Discriminations and AP in Oscines

One possible explanation of the superiority of zebra finches over chickadees in frequency-range discriminations is that zebra finches' songs are more broadband, that is, they include harmonics and cover a wider range of frequencies (see Sturdy, Phillmore, & Weisman, 1999) than chickadees' clearly whistled songs (see Ficken et al., 1978). The hypothesis is that experience with broader ranges of frequencies in songs improves frequency-range discriminations. This idea ignores the harmonics and the broad range of frequencies heard in the learned social contact *chick-a-dee* calls from which chickadees derive their name (see Charrier, Bloomfield, & Sturdy, 2004; Bloomfield et al., 2004). With chickadee calls factored in, the vocalizations of zebra finches and chickadees cover a remarkably similar range of frequencies and harmonics and therefore are unlikely to provide an explanation of differences in AP between these species.

Until we have evidence from a wider sample of species and more detailed evidence about the auditory sensitivity of these species (see Dooling & Okanoya, 1995), we can only speculate about the actual determinants of species differences in AP among oscines. From the evidence available so far, it appears that closely related species (e.g., black-capped and mountain chickadees) have more similar AP than more distantly related species (e.g., chickadees, white-throated sparrows, and zebra finches). Black-capped chickadees and white-throated sparrows produce high quality RP cues in their songs (Weisman & Ratcliffe, 2004; Hurly, Ratcliffe, & Weisman, 1990), whereas extensive studies of zebra finch song have not revealed any RP cues (e.g., Sturdy, Phillmore, & Weisman, 1999). Hence, it is tempting to link reduced AP with use of RP in oscines. Bioacoustic analyses of the songs of mountain chickadees could support or disprove the linkage hypothesis, depending on whether mountain chickadees do or do not produce RP cues in song. Also, artificial selection for singing in domesticated males may favor AP in zebra finches.

The causes of variability in AP observed among oscines aside, the evidence is now incontrovertible that oscines have remarkably accurate AP, which they use with alacrity to identify conspecifics

on the basis of their songs. Also, accurate AP in chickadees provides baseline control levels of accuracy for future studies of discriminations between the notes in their natural vocalizations.

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