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Black-Capped Chickadee (*Poecile atricapillus*) and Human (*Homo sapiens*) Chord Discrimination

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Human music perception is related both to musical experience and the physical properties of sound. Examining the processing of music by nonhuman animals has been generally neglected. We tested both black-capped chickadees and humans in a chord discrimination task that replicates and extends prior research with pigeons. We found that chickadees and humans, in common with pigeons, showed similar patterns of discrimination across manipulations of the 3rd and 5th notes of the triadic chords. For all species (chickadee and humans here, pigeons previously), chords with half-step alterations in the 5th note were easier to discriminate than half-step manipulations of the 3rd note, which is likely due to the sensory consonance of these chords. There were differences among species in terms of the fine discrimination of the chords within this larger pattern of results. Further, the ability to relearn the chords when transposed to a new root differed across species. Our results provide new comparative data suggesting some similarities in chord perception that span a wide range of species, from pigeons (nonvocal learners) to songbirds and humans (vocal learners).

Keywords: chord, discrimination, black-capped chickadee, human, biomusicology

Music is a universal and potentially unique feature of our species. All cultures have some form of music, and musical systems that developed in isolation from one another share many common elements such as logarithmic pitch scales and octave equivalence (notes doubled in frequency are perceived as the same; Dowling & Harwood, 1986). Music is a large part of human culture and archaeological research suggests it has been for at least 30,000 to 50,000 years (Kunej & Turk, 2000).

As a result, interest has grown in the developing field of biomusicology, an evolutionary approach to the scientific study of

music (Fitch, 2005; Hauser & McDermott, 2003; Justus & Hutsler, 2005; Trehub, 2003). Research in this field attempts to unravel the evolutionary origins of music through comparative research between human and nonhuman animals. This approach increases our understanding of the origins of the human musical faculty, what limitations and requirements there might be on perceiving/producing music, and what fundamental behavioral or physiological building blocks are present in nonhuman species that use auditory channels to listen and communicate. In many cases, songbirds have been chosen as subjects for comparative studies of

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music perception in animals because of the importance of acoustic communication to them (e.g., Hulse & Cynx, 1985; Watanabe, Uozumi, & Tanaka, 2005).

A significant body of research has explored songbird pitch perception. Pitch (perception of the fundamental frequency) is a critical component of music along with timbre (tone quality as perceived by the physical shape of soundwaves), amplitude (loudness), and temporal intervals. Pitch can be classified in one of two ways: relative pitch and absolute pitch. The former refers to the ability to perceive the relation between two or more notes. The latter refers to the ability to determine note pitch in the absence of any external referent. In many studies, songbirds appear to rely more on absolute rather than relative pitch to solve tasks designed with simple relative pitch relations (Cynx, Hulse, & Polyzois, 1986; Hulse, Cynx, & Humpal, 1984). A study that pitted absolute against relative pitch revealed that, although European starlings (*Sturnus vulgaris*) appeared to solve the task using absolute pitch as their primary strategy, the birds could use relative pitch to some extent. The switch to relying on relative pitch was especially evident when the test stimuli were from a range of frequencies that overlapped training stimuli (Hulse & Cynx, 1985). Subsequent studies have discovered that songbirds have highly developed absolute pitch perception abilities and perform much better than humans, pigeons, and rats on tasks that exclusively require absolute pitch (Weisman et al., 1998; Weisman, Njegovan, Williams, Cohen, & Sturdy, 2004; Friedrich, Zentall, & Weisman, 2007; for review see Weisman, Williams, Cohen, Njegovan, & Sturdy, 2006). In fact, fine-grained absolute pitch perception (typically measured as note naming) in humans is very rare and has been estimated to occur in less than one in 10,000 individuals (Bachem, 1955). Thus, the mechanisms underlying songbirds' perception of pitch intervals, which require the use of relative pitch, may be different from that of humans.

Besides looking at sequentially presented pitch relations, the notes forming these intervals can also be presented simultaneously. In this case, they form a harmonic complex that is the basis for chord perception in music. In particular, triads (three-note chords) play an important role in musical structure and organization. Birds have been found to be sensitive to such harmonic stimuli. Both java sparrows (*Padda oryzivora*; Watanabe et al., 2005) and starlings (Hulse, Bernard, & Braaten, 1995) that have been successfully trained to discriminate among triadic chords showed some transfer to other triadic chord stimuli presented at different absolute pitches where the relations among the notes in the triadic chord remained constant. In other words, they solved a task with harmonic chords that required the use of relative pitch.

Recently, members of our group tested a nonsongbird species, the pigeon (*Columba livia*), using a discrimination task involving more musically structured chords than previous studies of chord discrimination by birds (Brooks & Cook, 2010). The pigeons were trained to discriminate a major triadic chord (1st, 3rd, and 5th note from a major scale) from four other chords that were similar, except that either the 3rd or the 5th note of the chord was raised or lowered by one semitone. This generated four musical chords: the minor chord (minor), with a lowered 3rd note, the suspended 4th chord (sus4) with a raised 3rd note, the flat 5th chord (flat5), with a lowered 5th note, and the augmented (aug) chord with a raised 5th note. The major, minor, suspended 4th, and augmented chords are frequently used in various musical contexts. The flat5 chord,

although not normally used in western music without also flattening the 3rd to form a diminished chord, was tested to maintain consistency of design within the experiment (see Figure 1). Brooks and Cook (2010) found that pigeons and humans, when trained (or asked) to rate the similarity of these manipulated chords to the major chord, displayed similar patterns of responding. For instance, chords with manipulations of the 3rd note were rated as more similar to the major chord than chords having manipulations of the 5th note.

Here we report data from a chord discrimination study using the same stimuli and contingencies that were used by Brooks and Cook (2010) with both black-capped chickadees (*Poecile atricapillus*) and humans (*Homo sapiens*) as subjects. Black-capped chickadees are North American songbirds that, in common with other true (oscine) songbirds, have a complex, learned vocal system subserved by an interconnected set of definable brain regions (Ficken, Ficken, & Witkin, 1978; Shackleton & Ratcliffe, 1993; Hughes, Nowicki, & Lohr, 1998; Mooney, 2009). Thus songbirds, and their communication system, stand in sharp contrast to pigeons, whose vocalizations are unlearned and who lack a comparable neural architecture. Songbird vocal learning has often been compared to human vocal learning (e.g., Bolhuis, Okanoya, & Scharff, 2010; Doupe & Kuhl, 1999). More recently it has been suggested that vocal learners may be an ideal group for studying the evolution of music (e.g., Fitch, 2005; Patel, 2006) and evidence exists suggesting that vocal learners may share some essential components for music processing that are relatively rare, such as entrainment to a musical beat (Patel, Iversen, Bregman, & Schulz, 2009; Schachner, Brady, Pepperberg, & Hauser, 2009).

The purpose of Experiment 1 was to use the same stimuli from Brooks and Cook (2010) to compare a songbird's chord discrimination performance with that previously reported in pigeons. This provides a compelling comparison of chord discrimination and harmonic perception across very different orders of birds. In Experiment 2, we tested humans in an operant discrimination experiment comparable with those used to test pigeons and chickadees (i.e., with no verbal instructions) which permitted a more direct comparison between human and avian performance than the rating

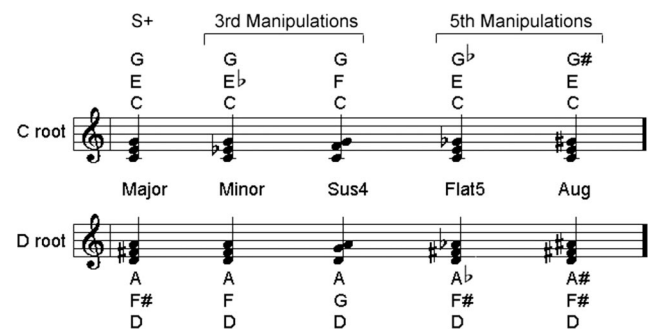


Figure 1. Musical notation of the chords used in both experiments. The top panel shows C root chords and the bottom panel shows the D root chords. Sus4 is the suspended 4th chord and aug is the augmented chord. Note names are provided above and below the musical notation. The major chord is labeled S+; all other chords are S- and are labeled either as manipulations of the 3rd (the middle note) or manipulations of the 5th (the top note). The 1st (root or bottom note) stayed constant throughout each discrimination.

task used by Brooks and Cook (2010). Our goal here was to conduct a systematic comparison of chord perception across species to determine how humans and avian species perceive musical chords. We had three main expectations: (1) that chickadees should be able to solve this chord task and do so more accurately than pigeons based on previous comparative pitch processing findings (Lee, Charrier, Bloomfield, Weisman, & Sturdy, 2006; Friedrich et al., 2007), (2) that human performance should be about equivalent to that of chickadees and superior to that of pigeons (Njegovan & Weisman, 1997; Weisman, Njegovan, & Ito, 1994), and (3) that chickadees, pigeons and humans have the same pattern of responding to all chords (responding that is primarily based on spectral properties of the chords rather than cultural influences e.g., modeled by N. D. Cook & Fujisawa, 2006).

General Method

Stimuli

Chords were generated using a French Horn synthesized MIDI timbre (Sonar 4, Cakewalk, Boston, U.S.A.). All stimuli were triads composed of notes selected from the fourth octave of the diatonic scale. For C root training, the S+ (reinforced or *go*) stimulus was the C major triad (C E G) while S- stimuli (nonreinforced or *no-go*) consisted of semitone deviations of either the 3rd or the 5th note of the C major chord in the following four variations: minor (C E^b G), sus4 (C F G), flat5 (C E G^b), and aug (C E G[#]). For D root training, the S+ stimulus was the D major chord (D F[#] A) while S- stimuli consisted of semitone deviations of either the 3rd or the 5th note of the D major chord in the following four variations: minor (D F A), sus4 (D G A), flat5 (D F[#] A^b), and aug (D F[#] A[#]). These chords were identical to those tested earlier with pigeons (Brooks & Cook, 2010), except that they were shortened and the edited portion tapered to 2-s total duration using SIGNAL version 5.10.24 (Engineering Design, Berkeley CA). This change made it possible to use the chords under our standard protocol (that requires chickadees listen to the entire stimulus before making a response) while maintaining the native attack and steady state portion of the stimuli.

General Procedure

Both chickadees (Experiment 1) and humans (Experiment 2) were trained using a Go/No-Go paradigm first to discriminate the C major chord from C minor, sus4, flat5 and aug chords. The C major chord was presented on 50% of the trials and was the rewarded stimulus. The other stimuli were presented approximately equally and together made up the other 50% of the trials which were unrewarded stimuli. The same discrimination was then conducted using the D root version of the same chords (discriminating the D major chord from D minor, sus4, flat5 and aug chords). The details of how this procedure was implemented in each species are described separately for each experiment below.

Response Measures

To determine whether the chickadees and humans had successfully learned to discriminate among the chords, we calculated a discrimination ratio (DR) between the S+ chord and each S-

chord. To calculate the DRs, we divided the percent response for the S+ chord by the sum of the percent response for the S+ chord and the S- chord of interest. A DR of 0.5 indicates equal responding to both S+ and S-, while a higher DR means more responding to S+ and a lower DR means more responding to S-. Percent response for chickadees was calculated by first excluding any interrupted trials from the total number of trials (see Experiment 1 procedure).

Experiment 1: Black-Capped Chickadees

Method

Animals

Six black-capped chickadees (three male and three female as identified by DNA analysis; Griffiths, Double, Orr, & Dawson, 1998) were tested between April and August, 2009. These birds were captured in Edmonton, Alberta, Canada (53°06' N, 113°04' W), and at the Barrier Lake Field Station in Kananaskis Country, Alberta, Canada (51°02' N, 115°03' W) between December 2007 and March 2008. All birds were determined at the time of capture to be at least one year of age by examining the color and shape of their outer tail retrices (Pyle, 1997). Prior to the experiment, all birds were housed individually in Jupiter Parakeet cages (30 × 40 × 40 cm; Rolf C. Hagen, Inc., Montreal, Canada) in colony rooms. The birds had visual and auditory, but not physical, contact with one another.

Throughout the experiment, birds were housed within individual operant chambers (see apparatus), maintained on the natural light cycle, and had ad libitum access to water, grit and cuttle bone. During experimentation, however, food was only available as a reward for correct responding in the operant discrimination task. Each chickadee had prior experience with auditory discriminations involving natural and synthetic stimuli (natural or synthetic *fee-bee* songs or *chick-a-dee* call note stimuli), but were naïve to the current stimulus set. For details about diet before and during the experiment, please refer to Guillette, Reddon, Hoeschele, and Sturdy (2011).

Apparatus

During the experiment, the birds lived in modified colony room cages (30 × 40 × 40 cm). Each cage was placed inside a ventilated sound-attenuating chamber and contained three perches and dispensers for water and grit. The chambers were illuminated by a 9-W, full spectrum fluorescent bulb. An opening on the side of the cage (11 × 16 cm) gave each bird access to a motor-driven feeder (Njegovan, Hilhorst, Ferguson, & Weisman, 1994). Both the feeder and the perch closest to the feeder (request perch) had infrared cells to monitor the position of the bird. A computer and single-board computer (Palya & Walter, 2001) scheduled trials and recorded responses to stimuli. Stimuli were played from CD through an amplifier and a full-range speaker located beside the feeder. For more equipment details, please refer to Sturdy and Weisman (2006). Stimuli were presented at amplitudes of roughly 76–82 dB as measured by a Radio Shack Sound Level Meter (A weighting, slow response; Radio Shack, Fort Worth, U.S.A.) from the position of each bird's head when located at the request perch.

Procedure

Nondifferential training. After a bird had learned to use the request perch and feeder, nondifferential training began. Trials continued indefinitely throughout the day cycle. Landing on the request perch, breaking the infrared beam and remaining for 1 s on average (range 0.9–1.1 s) initiated a trial. During each trial, one of the 10 chords (both C and D root) was randomly chosen without replacement from the pool and played through the speaker. Once all chords had been played in a random order, they were again randomized and the procedure repeated. If the bird left the perch during the 2-s playback of the chord (i.e., an interrupted trial), the chamber lights turned off for a 30-s intertrial interval (ITI), during which no new trial could begin. This ensured that the birds listened to the entire stimulus before making a response. If the bird flew or hopped to the feeder within 1 s after the completion of the stimulus, the bird received 1-s access to food. This was followed by a 30-s ITI with the chamber lights remaining on. If the bird left the perch upon completion of the stimulus but did not enter the feeder, the trial ended after 1 s and the bird could then initiate a new trial. To prevent each bird from sitting continuously on the request perch and initiating trial after trial, a new trial could only be activated by either leaving and returning to the request perch or waiting for a 60-s ITI. This increased the probability that a bird would make a response on a given trial. Data from this phase were evaluated in 500-trial blocks. Nondifferential training continued until birds were going to the feeder on a high proportion of trials (at least 60% of the trials) for at least six blocks and birds were responding with $\leq 3\%$ difference to future S + and S– chords for at least four blocks. This ensured there were no initial response biases to the stimuli.

C root discrimination training. C root discrimination training was identical to nondifferential training, but with several critical exceptions. During this phase, birds were only presented the C root chords. In addition, birds were rewarded only for responding, by entering the food hopper, following presentation of the S + C major chord. If they entered the feeder after an S– stimulus (all other C root chords), the chamber lights were turned off during a 30-s ITI. Finally, the reinforced (S+) C major chord made up 50% of the trials, while the four other nonreinforced (S–) C chords (i.e., alterations of the 3rd and 5ths) made up equal proportions of the remaining trials (12.5% each). Birds were trained with C root discrimination training until they each completed six 500-trial blocks (the last two occurring consecutively) in which Discrimination Ratio (DR) for each chord was greater than or equal to 0.80 (see response measures, above, for DR calculations). This took a variable number of trials for each bird, but ensured all birds were at the same level of expertise. The number of blocks taken to reach this criterion was subsequently used in our analyses (see statistical analyses section).

D root discrimination training. D root discrimination training commenced for each bird after criterion at C root training had been reached. This phase was identical to the C root discrimination training, except that the D chords were used as discriminative stimuli instead of the C chords. This was to test whether the birds could generalize the discrimination they learned about the C root chords to chords centered around a novel root note. The training criterion was the same as for C root discrimination.

Statistical Analyses

All analyses were conducted using Statistica version 8.0 (Statsoft Inc.). An alpha level of 0.05 or less was used to judge significance in statistical tests.

Acquisition. There was considerable variation among the birds in the number of blocks required to reach criterion for all chords (between 11 and 47 blocks depending on bird and discrimination training phase, either C or D root). For this reason, acquisition curves were standardized to Vincentized curves with 10 blocks of data so that we could compare the rate of acquisition across birds. Vincentizing was calculated by dividing the total number of actual blocks a bird did (e.g., 32) by 10 Vincentized blocks into whole numbers (in this example, 3 remainder 2). Vincentized blocks were then computed by grouping the total number of blocks a bird did into groups the size of the quotient (in this example, 3) and placing the any remaining blocks evenly into the middle two blocks (5th and 6th block, in this example, both the 5th and 6th block would have $3 + 1 = 4$ actual blocks grouped in) and then averaging the DR across grouped blocks (see Kling & Riggs, 1971). We conducted an analysis of variance (ANOVA) comparing the DR for Sex \times Vincentized blocks \times Chord type to see whether there were any differences in learning rates (e.g., if some chords are learned faster closer to the beginning of the learning curve). Additionally, to make our current work comparable to the previous pigeon work (Brooks & Cook, 2010) we conducted a similar analysis as that just described, but collapsing (1) minor and sus4 chords to compare acquisition with manipulations of the 3rd, and (2) the aug and flat5 chords to compare acquisitions with manipulation of the 5th.

Blocks to criterion. Because we tested all birds until they reached criterion at both stages for both C and D root training, we were able to evaluate the number of blocks to reach criterion for each individual chord discrimination (e.g., the minor from the major with a DR ≥ 0.8 for six blocks with the last two being consecutive). This was evaluated using a Sex \times Chord type ANOVA.

Savings. We also looked at whether there were any savings from C root training, to D root training. To complete this analysis, we calculated one-tailed z scores for each individual bird using binomial tests for dichotomous data to determine whether the proportion of responses that were directed to S + stimuli were significantly above chance (1/2 chance because 1/2 of the trials were S+) during the first block of each of the two discriminations (training and transfer).

Results

All birds reached criterion for each of the four comparison chord types in both C root and D root training. Figure 2 shows the average percent response across the 10 Vincentized blocks for each chord type for both C root (upper panel) and D root (lower panel) training. Figure 2 also shows that there is variation in the rate at which different S– chords are learned across acquisition. A more detailed depiction of the differences among S– chords is shown in Figure 3, where the number of blocks to reach criterion for each chord type and training phase are plotted for each individual bird. The pattern of results in Figure 3 suggests that the minor chord and the flat5 chords took the longest to learn during

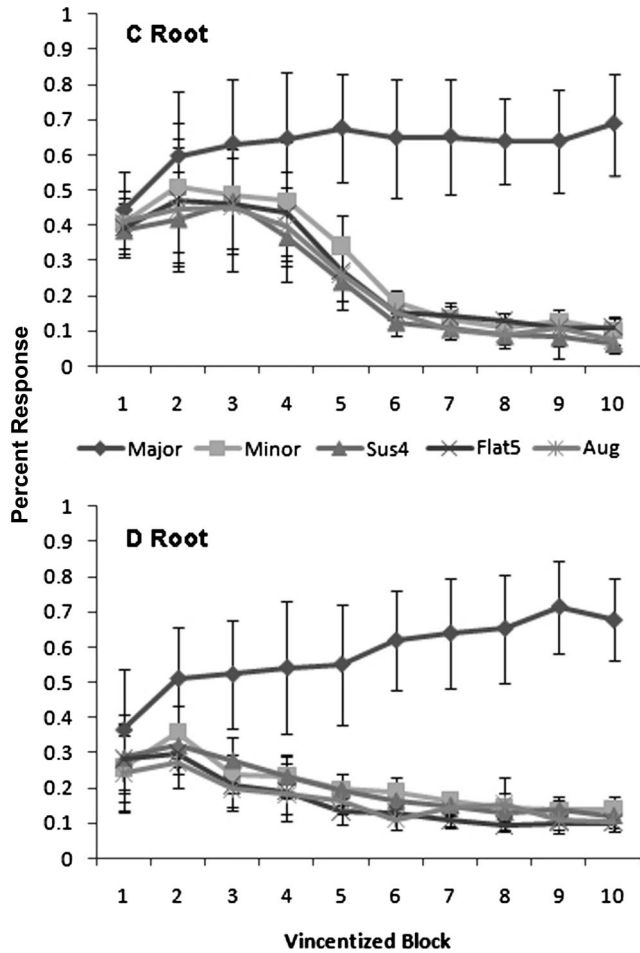


Figure 2. Average chickadee percent response for each chord across the 10 Vincentized blocks of C root training (top panel) and D root training (bottom panel). Error bars show 95% confidence intervals.

C root training, whereas the minor and sus4 chords took the longest to learn during D root training. In general, this pattern of results was supported by statistical analyses described below.

C Root Training

Acquisition. We found a main effect of Vincentized block in the ANOVA looking at the DRs of birds by Sex \times Vincentized blocks \times Chord type, both in the separated (minor VS sus4 VS flat5 VS aug) and collapsed (3rd manipulations VS 5th manipulations) versions of the analysis ($F(9, 36) = 72.78, p < .001$, partial $\eta^2 = 0.948$) where DR increased as Vincentized blocks increased. In the separated analysis, we also found a main effect of chord ($F(3, 12) = 10.90, p < .001$, partial $\eta^2 = 0.732$) that was not found in the collapsed analysis. Tukey post hoc tests show that the minor chord ($M = 0.70$) had a significantly lower overall DR than the aug chord ($M = 0.73; p = .015$) and the sus4 chord ($M = 0.75; p = .001$). In addition, the sus4 chord had a significantly higher DR than the flat5 chord ($M = 0.71; p = .010$).

Blocks to criterion. Figure 3 shows the blocks to criterion for each bird for each chord. All birds learned the minor chord last,

suggesting it took the longest to learn. Four birds learned sus4 first, one learned the aug chord first, and one learned both the aug and flat5 chords first. The analyses on blocks to criteria also showed results similar to the acquisition analysis. There was a main effect of chord ($F(3, 12) = 7.38, p = .005$, partial $\eta^2 = 0.648$). Tukey post hoc tests showed that the minor chord ($M = 27$) took significantly longer to learn than both the sus4 ($M = 22.33, p = .011$) and the aug chord ($M = 22.16, p = .009$), but not the flat5 chord ($M = 25.17, p = 0.464$).

D Root Training

Acquisition. We found a main effect of Vincentized block in the ANOVA looking at the DRs of birds by Sex \times Vincentized blocks \times Chord type, both in the separated (minor VS sus4 VS

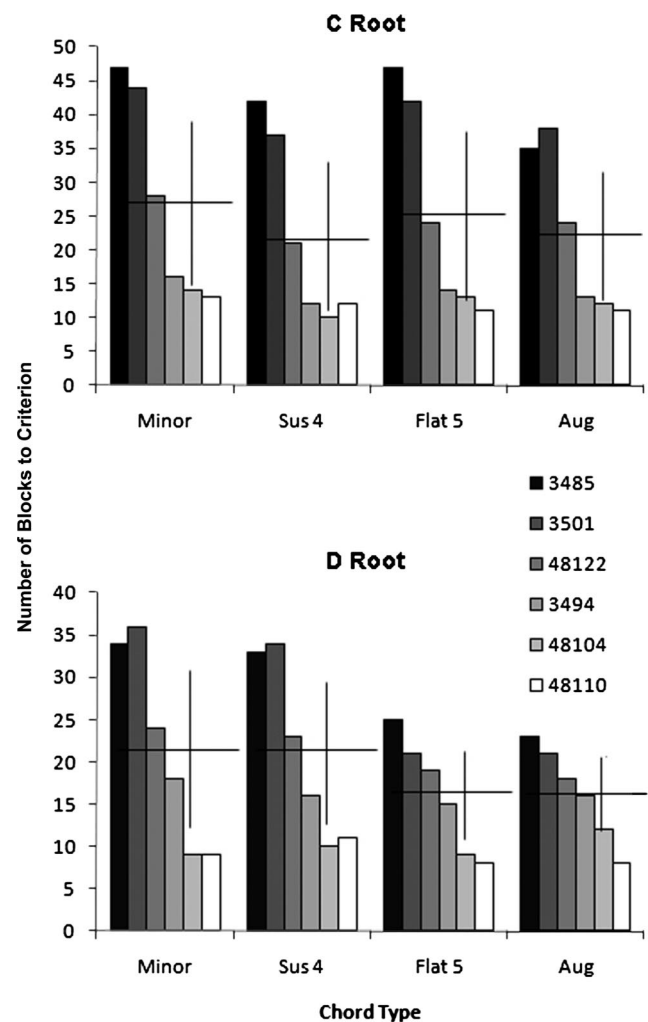


Figure 3. Total number of blocks required to reach criterion (a discrimination ratio of 0.8 compared to the major chord) for each comparison chord (minor, sus4, aug, and flat5) for all individual black-capped chickadees (labeled by subject id number). The top panel shows C root training and the bottom shows D root training. Crosses over each chord represent the mean and 95% confidence interval of the number of blocks required for each chord as comparison to the individual data.

flat5 VS aug) and collapsed (3rd manipulations VS 5th manipulations) versions of the analysis ($F(9, 36) = 36.96, p < .001$, partial $\eta^2 = 0.902$) where DR increased as Vincentized blocks increased. The main effect of chord did not reach significance in the separated analysis ($F(3, 12) = 3.20, p = .062$, partial $\eta^2 = 0.445$), however it was significant in the collapsed analysis ($F(3, 12) = 34.89, p = .004$, partial $\eta^2 = 0.897$). The collapsed analysis results suggests that, during D root training, the birds learned the 5th manipulations (aug $M = 0.77$; flat5 $M = 0.77$) to a higher DR than the 3rd manipulations (minor $M = 0.73$; sus4 $M = 0.73$).

Blocks to criterion. Figure 3 shows the blocks to criterion for each bird for each chord. Four of the six birds learned to discriminate the minor chord from the major chord last, and the other two learned to discriminate either the aug or the sus4 chord from the major chord last. All birds except one learned to discriminate one or both of the 5th manipulation chords from the major chord first (flat5 and aug); one bird learned to discriminate the flat5 and minor chord from the major chord first. The analyses on blocks to criteria showed that there was a main effect of chord ($F(3, 12) = 4.61, p = .023$, partial $\eta^2 = 0.535$). However, Tukey post hoc tests showed no significant differences between the chords, although the minor chord ($M = 21.67$) approached a significantly longer learning time compared to the flat5 ($M = 16.17, p = .068$) and aug ($M = 16.33, p = .078$) chord, but not the sus4 chord ($M = 21.17, p = .994$). This suggests that the chords that had lower DRs may also have taken longer to learn.

Savings

Figure 2 shows acquisition of the initial C root discrimination (upper panel) and the subsequent D root discrimination (lower panel). A comparison of the pattern of responding to S + and S- stimuli in the early stages of each panel suggest that training from the C root discrimination aided in solving the subsequent D root discrimination. That is, there appeared to be savings in the D root discrimination such that responding to S + and S- chords was already diverging early on in training by comparison to that seen in early trials of C root training. On average, the DRs during the first block of D root training appeared higher ($M = 0.58$) compared to C root training ($M = 0.51$). The same was true for the individual chords (C minor $M = 0.52$, D minor $M = 0.59$; C sus4 $M = 0.51$, D sus4 $M = 0.58$; C flat5 $M = 0.51$, D flat5 $M = 0.53$; C aug $M = 0.50$, D aug $M = 0.61$). Only one bird was at criterion within the first block of D root training (i.e., had a DR ≥ 0.80) for two of the four chords (aug and sus4), which also had the best average performance the end of the C root training.

The binomial tests for dichotomous data showed that while only one bird was above chance during the first block of the C root discrimination (bird 48110 required the fewest blocks to complete the discrimination; $z = 1.90, p = .029$), three birds responded above chance during the first block of the D root discrimination (all z s ≥ 2.29 , all p s ≤ 0.011). Thus it appears that there was savings of the C root discrimination to the D root discrimination, although only for half the birds, which is less than what was seen in some previous work with biologically relevant stimuli (e.g., Bloomfield & Sturdy, 2008; Guillette, Reddon, Hurd, & Sturdy, 2009).

Experiment 2: Humans

Method

Nineteen undergraduate students (ages range 18–22 years; 15 reported private lessons in musical training, two reported no private lessons but group lessons or self-taught ability in music) at the University of Alberta completed the task for course credit.

Apparatus and Stimuli

Participants were tested using a laptop computer (Toshiba Tecra, Intel Pentium M processor and Intel 855 series chip set) equipped with Sennheiser HD 580 headphones. Computer software (programmed in Visual Basic) tested the participants in a task directly comparable to the chickadees in Experiment 1 using identical chord stimuli. Participants had the option of adjusting the volume to a comfortable level using a dial at the front of the laptop (see Weisman et al., 2010).

Procedure

After completing a survey about musical training, participants were trained to discriminate the major chord from the four comparison chords used in Experiment 1. S + and S- trials were selected randomly an equal number of times within each test: the major chord was played 48 times, and all other chords were played 12 times each for a total of 96 trials. Each participant completed this test, first with the C root chords and then with the D root chords.

The first 10 of the 19 participants completed each C and D root chord training twice. At that point, we found that all participants were successfully discriminating the C chords by the end of the first test. Thus, subsequently, we had participants perform each test only once. We found no statistical differences between participants who completed one or two tests. Thus, the data for all 19 participants were collapsed and only the first test used for all analyses.

Participants initiated a trial by clicking on the “play” button on the screen to hear a chord. If the major chord played and the participant pressed a button labeled “S+” the word “correct” appeared in a box adjacent to the S + button as visual feedback. If the participant clicked the S + button for any other chord, the word “incorrect” appeared in a box adjacent to the S + button and the next trial was delayed by 5 s. Participants were told that sounds had been placed in two categories, but were given no hints as to how to categorize the sounds.

Statistical Analyses

All analyses were conducted in Statistica version 8.0 (Statsoft Inc.). An alpha level of 0.05 or less was used to judge significance in statistical tests.

Overall performance. We evaluated performance by comparing the DRs for each chord calculated for all 96 trials within subjects using sex as a between-subjects categorical variable in an ANOVA for both C root and D root training. This analysis was repeated collapsing the chords into 3rd manipulations (minor and sus4) and 5th manipulations (aug and flat5) to make it directly comparable to previous pigeon work (Brooks & Cook, 2010) and Experiment 1 with the chickadees.

Savings. We also looked at whether there were any savings from C root training for individuals by testing the proportion of responding to the first exposure of the S- chords in C and D root training against chance (0.5) using single sample *t* tests.

Results

Participants learned the task extremely quickly (often within the first two exposures to each chord type; see Figure 4). All participants met criterion for the first test (C root) except one. This one participant expressed confusion after completing the task and pressed go on almost every trial (94/96 trials), and as a result this participant's data were excluded from the analysis. All other participants were above 0.8 DR for at least two of the four chords during the 96 trial block and only three participants had DRs for any chords that were less than 0.7.

Overall Performance

C root training. During the C root training, we found a main effect of chord ($F(3, 14) = 4.61, p = .007$, partial $\eta^2 = 0.224$). Mean DR for the different chords types across the 96 training trials

were flat5 ($M = 0.93$), aug ($M = 0.89$), minor ($M = 0.86$), sus4 ($M = 0.84$). We conducted dependent *t* tests to determine the particular differences among the chord types underlying the main effect of chord. We found that the flat5 chord had a significantly higher DR than both the sus4, $t(17) = 3.26, p = .005$, and the minor, $t(17) = 3.20, p = .005$, chord. The collapsed analysis confirms this pattern and shows a main effect of chord type, such that 3rd manipulations ($M = 0.85$) were more difficult to discriminate compared to 5th manipulations ($M = 0.91; F(1, 16) = 12.53, p = .003$, partial $\eta^2 = 0.439$).

D root training. During the D root training, a similar pattern emerged compared to C root training. There was a main effect of chord ($F(3, 14) = 6.51, p = .001$, partial $\eta^2 = 0.289$). The degree of learning appeared to be similar when comparing DRs for the flat5 ($M = 0.98$), aug ($M = 0.96$), minor ($M = 0.95$), and sus4 ($M = 0.90$) chords. We conducted dependent *t* tests to determine the particular differences among the chord types underlying the main effect of chord. We found that the sus4 chord had a significantly lower DR than both the flat5, $t(17) = 3.47, p = .003$, and aug, $t(17) = 3.04, p = .007$, and minor chord, $t(17) = 2.31, p = .034$. The minor chord also had a significantly lower DR than the flat5 chord, $t(17) = 2.40, p = .028$. The collapsed analysis supported this further with a main effect of chord type ($F(1, 16) = 11.45, p = .004$, partial $\eta^2 = 0.417$) where manipulations of the 3rd ($M = 0.92$) had a lower average DR than manipulations of the 5th ($M = 0.97$).

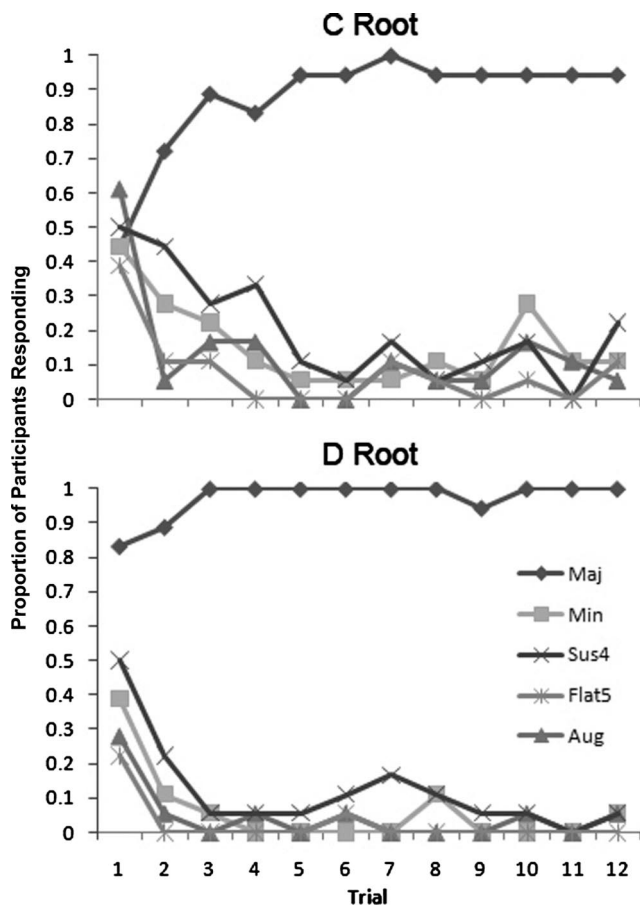


Figure 4. Proportion of human participants that responded to each chord type during the first 12 trials with each chord. Participants heard the comparison chords (minor, aug, sus4 and flat5) 12 times each and the major chord 48 times. The top panel shows responding during C root training and the bottom shows D root training.

Savings

We compared the proportion of responding during the first exposure to all S- chords by each individual (i.e., collapsing across chord) for D root training against chance, and we found a significant difference, $t(17) = 2.17, p = .045$, which we did not find when comparing the proportion of responding during the first exposure to S- chords by each individual for C root training against chance, $t(17) = 0.20, p = .842$. Indeed, in Figure 4, one can already see the separation of the S+ and S- chords in trial one for the D root training, which is not the case for C root training.

Comparative Analysis

In order to make the results from the chickadees and humans in our study and the previously studied pigeons more directly comparable, we plotted the proportion of errors to each S- chord for each species (see Figure 5). For chickadees, we used the proportion of errors in the final Vincentized block of acquisition. For humans, we used the proportion of errors across the whole session because of how quickly they learned the task. For pigeons, we used the proportion of errors once they reached a steady state of responding (see Brooks & Cook, 2010). The figure shows that pigeons and humans were very similar in both the rank order (sus4 was the most difficult, followed by the minor, aug and the flat5) and magnitude of their errors during C root training, while chickadee errors were less to the sus4 chord and more to the flat5 chord than the other two species. In D root training, pigeons and humans continued to follow the same pattern of which chords were the most difficult, but with more variable magnitudes. Chickadees continued to differ in the order of most to least errors from the

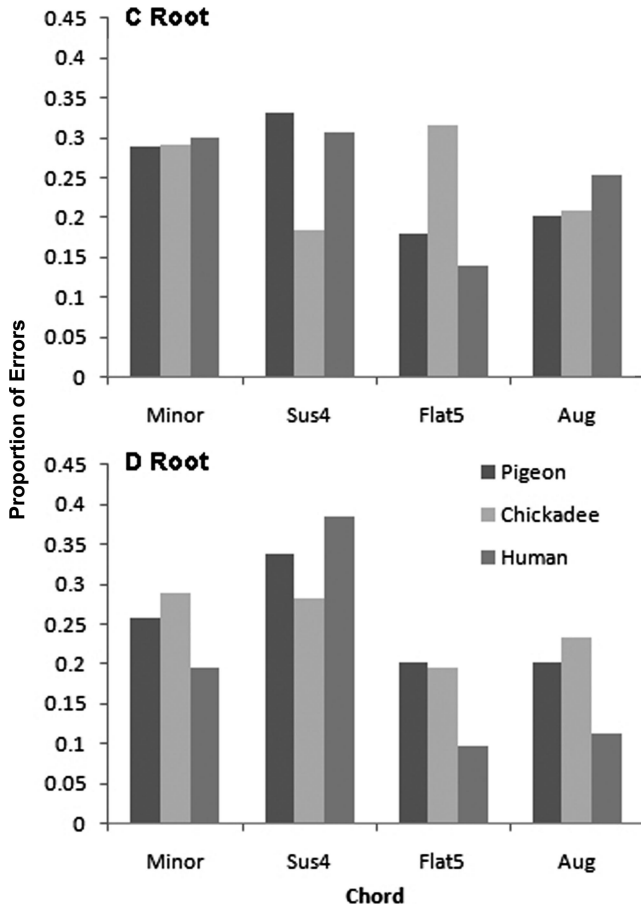


Figure 5. The proportion of errors to each S– chord for each of the three tested species on our chord protocol: pigeons, chickadees and humans. The top panel represents C Root Training errors and the bottom panel represents D Root Training.

other two species in that the sus4 was not as difficult as the minor chord to discriminate for the chickadees.

Discussion

Here we show that both black-capped chickadees and humans are able to discriminate triadic chords with the same root. In contrast to the previous work with pigeons, all chickadees learned to discriminate these chords, whereas only a subset of pigeons were able to learn the discrimination (Brooks & Cook, 2010), as was also the case in other avian studies with chord stimuli (e.g., Watanabe et al., 2005; Hulse et al., 1995). For all three species (humans, chickadees, and pigeons) now tested with this set of common chord stimuli, manipulations of the 3rd note (minor and sus4 chords) are more difficult to discriminate from the major chord than chords with manipulations of the 5th note (aug and flat5 chords). However, more detailed comparisons among the individual chords creates a more complex picture.

We expected that humans and chickadees would both be able to solve the task and exhibit similar patterns of discrimination with one another. In a general sense, this is true: both humans and chickadees are able to discriminate among stimuli with complex

harmonic structures and do so in a comparable manner. However, there are subtle differences that may reflect different ecological niches for the different species. For example, differences in the rate of acquisition in chickadees are likely a function of the key or absolute pitch of the chords (i.e., whether they were C or D root chords). This is a possibility because songbirds are very adept at absolute pitch processing and have no trouble distinguishing tones that differ by roughly a semitone (Weisman et al., 1998; Weisman et al., 2004; Friedrich et al., 2007; for review see Weisman, Williams, Cohen, Njegovan, & Sturdy, 2006). For instance, chickadees found both 5th manipulations clearly easier to discriminate when the root note was D, but not when the root was C. When the root was C, the sus4 chord (3rd manipulation) was relatively easy for them to discriminate, and the flat5 was relatively more difficult for them to discriminate. This differential responding depending on the root of the chord was not found in either humans or pigeons, who generally responded similarly to the four chord types regardless of the root note (but see Brooks & Cook, 2010, for some exceptions in pigeons). However, this effect in chickadees may be partially due to the fact that all birds were trained first with C root chords and then D root chords. This suggests that the absolute pitch of the notes may be affecting the manner in which chickadees process complex auditory stimuli, a common finding in studies of auditory perception in songbirds (Cynx et al., 1986; Hulse et al., 1984; Njegovan & Weisman, 1997). However, it is also possible that humans are similarly affected by changes in absolute pitch, but their strong reliance on relative pitch masks any differential responding based on absolute pitch. Part of this reliance of relative pitch by the human participants in our study could be affected by the fact that western music has an equally tempered scale (i.e., all notes are separated by the same distance). This is potentially relevant because it means that different keys (e.g., C major or D major) make use of the same relative pitch ratios and make absolute pitch less important than in a musical system with an unequally tempered scale. The exact reason for the differences among species is at the moment not clear, especially given that pigeons seem to be responding more similarly to humans than chickadees. This is somewhat surprising since humans and chickadees, but not pigeons, are vocal learners (see Tyack, 2008 for a recent review of vocal learners) and songbirds and humans have similar vocal learning behaviors, and neural pathways underlying vocal production (Doupe & Kuhl, 1999). Songbirds are also thought to share perceptual abilities required for musical perception such as rhythm perception (see Schachner et al., 2009), an ability with which pigeons struggle (Hagmann & Cook, 2010).

The chickadees also consistently found the minor chord the most difficult to discriminate from the major chord, while humans consistently found the sus4 the most difficult to discriminate from the major chord. This may be due to musical experience in the humans we tested, because the minor chord more commonly occurs in western music than the sus4 chord. Further support from this comes from the fact that the sus4 introduces novel intervals between the notes, compared to the major chord, which the minor chord does not. Specifically, the 3rd note in the major chord forms a major 3rd with the 1st note and a minor 3rd with the 5th note. In the minor chord, these relationships are swapped such that the 3rd note makes a minor third with the 1st note and a major 3rd with the 5th note. The 3rd note in the sus4 chord, on the other hand, forms a perfect 4th with the 1st note and a major 2nd with the 5th note.

The perfect 4th is considered more consonant and the major 2nd less consonant than either 3rd interval (major and minor 3rds; Rasch & Plomp, 1999). To an animal that has little to no experience with western music it is possible therefore, that a sus4 would be easier to discriminate. However, the pigeons also showed much more difficulty in discriminating the sus4 chord from the minor in C root chords, suggesting that there might be something else at work here. One possibility is that the chickadees may have found the sus4 chord easier to discriminate because the sus4 includes a major 2nd interval, which is very close to the interval used in their song to advertise male quality (Christie, Mennill, & Ratcliffe, 2004).

Despite the differences, however, when we compare overall responding to the chord types regardless of root (see bottom panel of Figure 5), the species do respond similarly, with 3rd manipulations being more difficult than 5th manipulations. One possible explanation for the similar overall responding across all three species may be related to the perceived consonance and dissonance of the different chord types. Helmholtz (1877) originally proposed that pitch intervals were either consonant or dissonant because of the simplicity or complexity of the relationships of the harmonics. He pointed out that dissonant intervals, such as the minor second or major seventh, have few shared harmonics and their harmonics often are close, creating a roughness or beating sound that musicians listen for when tuning an instrument. On the other hand, perfect intervals such as a perfect 5th (ratio of 2:3) and octave (ratio of 1:2), have simple relations with many shared upper harmonics and are perceived more like a single note. If this is the case, it may be that we would not have found the same results had we used pure tones for the creation of the chords because of their lack of upper harmonics. Testing with pure tones may be a potential route that might lead to further insight on this matter. However, pure tones are thought to have a similar effect to that of harmonics because of the matching of phase information for neural firing patterns (Burns, 1999), so it may not matter whether or not pure tones are used.

A potential problem with Helmholtz' definition of consonance and dissonance is that this does not fully correspond to how humans treat the chords in many experiments, including the current study. By Helmholtz' reasoning alone, the aug chord should sound relatively consonant because of the simple harmonic relationships among the notes, but this is not what is generally found. Other factors are thought to contribute to consonance and dissonance, but there are no agreed upon definitions. One model of consonance and dissonance that seems to accurately reflect ratings of consonance and dissonance across cultures and therefore may be of greater universal significance is N. D. Cook and Fujisawa's (2006) model. In addition to beating harmonics, they take into account the "tension" of the chord in deriving the formulas for their model. A chord is thought to be more tense if the intervals between all notes are similar than if they are different (e.g., the relations of the 3rd to the 1st and 5th note of the aug chord are both major 3rds i.e., both four semitones apart). A more tense chord is also more dissonant and this may be because of cognitive grouping mechanisms whereby it is more difficult to group tones based on relative distance when all distances are equal (Cook & Fujisawa, 2006). This fits well with our current results for both humans and black-capped chickadees, as well as the previous results with pigeons, who found the aug chord was quite different to the major

chord, despite the similar consonance according to Helmholtz' definition. In fact, the avian species found this chord especially easy to discriminate regardless of the absolute pitch of the chords.

One future avenue for our research would thus be to systematically alter the tension and relationship of the upper harmonics in intervals to examine what controls consonance and dissonance in both humans and other animals. Because humans from different musical cultures have variations in what they perceive as consonant and dissonant (Carterette & Kendall, 1999), animal research may be able to address which potential factors contributing to musical perception are cultural influences, and which are fundamental components of complex auditory processing.

Another important consideration for our study is that all chord changes were being evaluated against the major chord and not directly against perfect consonance. The 3rd in the major chord forms a major 3rd interval and a minor 3rd interval between the 1st and 5th note respectively, while the 5th note forms a perfect 5th and a minor 3rd, with the 1st and 3rd note respectively. The frequency of the notes forming a perfect 5th have a ratio of 2:3 and this interval is considered the most consonant interval after unison and the octave. Major and minor 3rds, while still considered consonant, are thought to be less consonant in comparison to the perfect intervals (Rasch & Plomp, 1999). Thus, part of the reason the 5th alterations were easily differentiable from the major chord is potentially because of the greater change along a consonance/dissonance continuum.

By using complex musical chords as stimuli, the current experiment also provided additional insight into how chickadees perceive auditory stimuli. One example of this is the observation of savings when the root changed from C to D. Half the chickadees show savings with a DR higher than chance in the first block of D root training, and one chickadee reached criterion for some chords within the first 500-trial block (sus4 and aug chord). It may therefore be possible for chickadees to more heavily rely on relative pitch rather than absolute pitch in some circumstances; however it could also be that chickadees are simply learning the second discrimination more rapidly because they learned what types of differences to attend to among chords. In other words, if we had presented a second group of birds with a D root chord task that used chords with different relative pitch relations, would this have been learned as rapidly? This is something that we are interested in investigating further. All birds in our experiment were able to learn the chords with sufficient training, which is different from the previous work with sparrows, starlings, and pigeons (Watanabe et al., 2005; Hulse et al., 1995; Brooks & Cook, 2010). It may be that chickadees in particular are better at relative pitch tasks because they attend to relative pitch cues in their song (Weisman, Ratcliffe, Johnsrude & Hurly, 1990; Weisman & Ratcliffe, 2004; Christie et al., 2004). However, past research with descending intervals suggests that it can be very difficult to train black-capped chickadees on relative pitch tasks (Njegovan & Weisman, 1997). It is possible that, because our current task presented all notes simultaneously, that the chickadees were better able to use relative pitch rather than memorizing the absolute pitch of one of the notes. Further training with more chord sets using different roots could lead to insight on the matter of whether chickadees are better able to switch to using relative pitch for pitch categorization than previously assumed. Additionally, comparisons between presentations of harmonic chords, where all notes are

played simultaneously, and broken chords, where notes are played individually, may reveal that the apparent reliance on absolute pitch in songbirds may not be due to a preference for absolute pitch processing, per se, but rather could be rooted in the demands of the tasks such as attentional or memory differences among experiments. To date, most studies looking at relative mechanisms in chickadees (Njegovan & Weisman, 1997) and other songbirds (Cynx et al., 1986; Hulse et al., 1984) have used broken chords rather than harmonic chords.

There are several broad implications of our comparative perceptual work with musical stimuli. As West, King, and Goldstein (2004) suggest, music may be a building block of vocal communication shared across a wide variety of taxa. Masataka (2009) further supports this claim by suggesting that a primitive form of modern human music was potentially the foundation of both modern music and language in humans. It is possible that there may be an underlying mechanism of consonance and dissonance that is present across all cultures based on properties of chords (see model by N. D. Cook & Fujisawa, 2006) and the perception of these properties appear to also be predictable by the structure of human speech (Schwartz, Howe, & Purves, 2003). This evidence, along with evidence suggesting that pitch intervals may be used to convey similar messages in speech (at least the minor interval; Curtis & Bharucha, 2010), suggests that consonance and dissonance may have an evolutionary basis rather than simply being a human cultural phenomenon. By studying both other mammals, especially other primates, and distantly related both vocal learning and nonvocal learning animals, we can begin to tease apart what parts of our musical perception are fundamental components of auditory perception in all hearing animals, and what parts of musical perception are required for complex auditory processing (analogous) or present only in closely related species (homologous). Because of how similarly pigeons and humans responded compared to chickadees, our results potentially suggest that more fundamental auditory processing components found in a nonvocal learning pigeon are found in both humans and chickadees, and a higher-level ecologically relevant component may be influencing the further differences among chickadees (e.g., species specific vocalizations) and humans (e.g., cultural influences).

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