CHORD DISCRIMINATION BY PIGEONS

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PIGEONS WERE TRAINED IN A GO/NO-GO TASK TO discriminate a major triad from four other chord triads. These latter chords were constructed by altering the third or fifth of the triad by one semitone, creating minor, suspended fourth, augmented, or flat five chords. Experiment 1 used a C root to test these chords. Experiment 2 examined the discrimination of these chords using the D root. Pigeons could discriminate these harmonically complex triads, with manipulations of the fifth supporting better discrimination than manipulations of the third. The augmented chord was perceived as the most dissimilar from the major chord and the suspended fourth chord as the most similar. A combination of attention to sensory consonance and absolute properties of the chords is suggested to account for the results. Comparable human results suggested some overlap in their perception of harmonic elements, but a considerable difference in their flexibility to use this information across different contexts.

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MUSIC IS ONE OF THE COMMON QUALITIES SHARED by nearly all humans and is possibly a defining characteristic of our species. The production and perception of music is foundational to human culture, and it has powerful effects on our thoughts and emotions. It is very unlikely that all of the cognitive processes required for the perception of music spontaneously formed in our hominid ancestors (Kunej & Turk, 2000; Wallin, Merker, & Brown, 2000). The melodic, harmonic and rhythmic components that form human music must have had some cognitive precursors in non-human primates, and potentially other animals, prior to their emergence and flowering in our species. Thus, thoughtful speculation about the origins and evolution of music perception and its function in human behavior demands a comparative perspective that has generally been missing and underexamined. Recent reviews of music perception (Fitch, 2005; Hauser & McDermott, 2003; Justus & Hutsler, 2005; Trehub, 2003) have strongly encouraged the greater study of music in non-human animals. Such studies would help to bridge important gaps in our understanding of music, how music evolved to its present day competency, what perceptual or cognitive mechanisms are required for music perception and production, and the possible evolutionary relations between music, language, and the brain.

Experiments on music perception in animals have tested a number of species, from songbirds to primates, to examine the putative fundamental processes required to perceive the relationships inherent in musical structure. This work has ranged from attempts to establish the basics of auditory physiology as they might relate to music perception (e.g., McKenna, Weinberger, & Diamond, 1989), to behavioral experiments aimed at establishing whether animals can discriminate between pieces and styles of music (Porter & Neuringer, 1984; Watanabe & Sato, 1999). Still other experiments have attempted to map the similarities between human and animal music perception. For example, Wright, Rivera, Hulse, and Shyan (2000) found that rhesus monkeys (*Macaca mulata)* showed evidence of octave generalization, with monkeys more likely to choose a "same" choice to octave-shifted melodies than to melodies shifted to other keys.

One fundamental aspect of music involves the melodic and harmonic perception of musical intervals. Interval perception has been one of the most productive areas of research in human musical cognition because it is so critical to the way we perceive the similarities between individual pitches and melodies. Researchers have studied the influence of interval perception on key distance (Trainor & Trehub, 1993), melodic similarity (Cuddy, Cohen, & Mewhort, 1981; Sloboda & Edworthy, 1981), consonance judgments (Schellenberg & Trehub, 1996), and scale perception (Trehub, Schellenberg, & Kamenetsky, 1999).

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Several of these intervals are particularly important because they form the harmonic building blocks of triadic chords (Cook & Hayashi, 2008). In simple chords, the first, third, and fifth diatonic tones of a scale are stacked to create configural combinations that are basic to music. In all types of music, such chords create a set of relations that identify the structure and the mode of a musical piece and their sequential progression often creates the tension and resolution required of good music (Bharucha & Stoeckig, 1986). In this study, we wanted to examine for the first time how an avian non-songbird, the pigeon (*Columba livia*), perceives and discriminates chords of various structures and how the interval content of these chords influenced this discrimination.

The very small amount of prior research with songbirds has suggested that chords and interval content can form the basis of an auditory discrimination. Hulse, Bernard, and Braaten (1995) examined whether European starlings (*Sturnis vulgaris*) could discriminate in a choice task between a major triad, consisting of the first, third, and fifth tones of a scale, and a second chord type, consisting of the first, second, and fifth tones. Four of six starlings were able to learn this discrimination, and with significant additional experience transfer this discrimination to new root notes within a 200 Hz range. The successful starlings also were able to transfer this discrimination to inverted training chords. Some of the starlings also were able to transfer or rapidly learn a new discrimination with two new chords consisting of rather non-standard intervals. Hulse et al. suggested that perhaps the best account of their results was that the starlings may have learned to attend to the consonance and dissonance of the chord types.

More recently, Watanabe, Uozumi, and Tanaka (2005) reported that Java sparrows (*Padda oryzivora*) seemed able to discriminate between consonant or dissonant chords. Four of six sparrows learned to discriminate between a consonant set of three diatonic major chords and one minor chord, and a dissonant set of four chords composed of different combinations of smaller intervals. The four successful sparrows transferred to new examples of these chord types in one test, but not to chord inversions in a second test. A third transfer test with new dissonant chords produced mixed results. They similarly conclude that Java sparrows may be able to discriminate between the consonance and dissonance of different chords.

In this article, we report two new experiments investigating the role of interval structure in the discrimination of triadic chords by pigeons. This research was part of a general effort to better understand how these animals perceive and process acoustic stimuli when presented in more complex relations (Cook & Brooks, 2009; Murphy & Cook, 2008). Besides being non-songbirds, pigeons are an interesting animal to study because they have had no obvious evolutionary pressure to appreciate the structure of human music. Pigeons have an unlearned vocabulary of about five basic vocalizations and sounds that are used in social interactions, such as mating and breeding (Baptista & Abs, 1983). Some of these vocalizations have a complex and functional harmonic structure. The evaluation of their capabilities to perceive harmonic structures advances our understanding of music by outlining what musical fundamentals or capabilities may be language independent and widespread, and thus potentially more primitive, across the animal kingdom.

Besides testing a non-songbird for the first time, we also wanted to examine more carefully how the specific interval content of the chords influenced discrimination in comparison to these earlier studies on avian chord discrimination. While both of the previous studies had used major chords as a part of their initial discrimination, they had opposed them with rather non-standard and often non-musical chord structures, at least from a human perspective. We tested the pigeons with chord types that appear frequently in musical contexts. We chose to test harmonic relations, rather than melodies, because sensitivity to melodic information in a sequence of pitches requires the integration of pitch relations across time. As a result, the perception of melodies, rather than chords, involves the use of some form of short-term memory mechanism. Pigeons are certainly capable of doing this (Cook & Brooks, 2009) and looking at "melodies" is highly interesting, but we thought that eliminating any temporal component would be the simpler place to begin. The chosen chords were structured to allow us to examine specifically how the third or fifth intervals in the chords contributed to performance. In Experiment 1, the pigeons were trained with chords constructed from the C major scale. For all pigeons, the positive S+ chord was the major triad. Pecks during the playing of this chord resulted in food reinforcement on a variable interval schedule. Four other chords were used as S– stimuli. Pecks during the playing of these chords were never reinforced. The difference in resulting peck rates between the reinforced positive and non-reinforced negative conditions allowed for an assessment of how well the animals discriminated the differences between these stimuli and provides an index of their relative similarity (cf. Astley & Wasserman, 1992; Cook, Kelly, & Katz, 2003).

The S+ chord type was chosen to be the C major chord, the most common chord in Western music, from which a number of fundamental and functional chords can be easily derived with only single note changes. The four S– chord types were constructed in the following way. Two involved semitone or half-step manipulations of the tone making the third interval. In one case, the third was flatted resulting in a standard minor chord. This is by far the second most common chord type in music and this interval change is the defining cue between major and minor modes of Western music. The other chord type involved raising the third a half step to make an interval based on the fourth tone. This forms a suspended fourth (sus4) chord, a frequently used chord in rock music. It is generally viewed as consonant with a major chord. The other two chords tested involved half-step manipulations of the fifth interval. In one case the fifth interval was flatted. This triadic interval most typically occurs in music with a flatted third to form a diminished chord, but was tested here in this form to be consistent with the overall design of the experiment. This unorthodox chord will be referred to as the flat five chord. The last chord involved raising the fifth a half-step to create an augmented chord, a chord that frequently occurs in jazz music. Using this design, we were able to test if the pigeons could learn to discriminate chords and how different intervals contributed to the discrimination.

Experiment 1

Experiment 1 tested the pigeons with these five chords using a C root. In each daily session, the pigeons were reinforced for pecking during the C major chord and not reinforced for pecking during the four other chord types derived from this root. By measuring the pigeons' relative rate of pecking during presentations of the five different chord types tested, we could get a measure of similarity among these stimuli relative to the C major chord. The pigeons were trained for fifty sessions using this procedure.

Method

ANIMALS

Five male pigeons were tested. All were naïve with respect to auditory discriminations. Four had previous experience in different visual discrimination tasks. They were maintained at 80-85% of their free-feeding weights in a colony room with a 12:12 light-dark cycle and had free access to water and grit in their home cages.

APPARATUS

Testing was done in a flat-black Plexiglas chamber (42.5 cm wide, 44 cm deep, 39.5 cm high). All events were controlled by a computer. The visual stimuli were presented on a color monitor visible through a 25.5 cm × 21.5 cm opening in the middle of the chamber's front panel. Pecks were detected by an infrared LED touch screen (Carrol Touch, distributed by EloTouch) that formed the window. The auditory stimuli were presented from bilateral two-way speakers (HK-195, Harmon-Kardon; frequency range 90 Hz to 20 KHz) located in the front edges of the left and right walls of the chamber. The stimuli were generated by an integrated sound card (SoundMax). A houselight was located in the ceiling of the chamber and was illuminated at all times, except during timeouts. Mixed grain was delivered by a food hopper that was centrally located in the front panel below the opening.

STIMULI

Auditory stimuli were software generated (Sonar 4, Cakewalk) synthesized waveforms that were played as WAV files. The "french horn" setting, a synthesized MIDI timbre within the software was used to create the stimuli. We had used this timbre in an earlier study (Cook & Brooks, 2009) and it was readily discriminated by the pigeons. Further, the timbre of the french horn has a rich harmonic structure that makes the global processing of its configuration highly likely in comparison to some other instruments. The stimuli were triads composed from notes selected from the third octave of the diatonic scale (C root note = 130 Hz). The C major chord (C, E, G) was chosen as the reinforced (*go*) stimulus. The four other chords served as the non-reinforced (no-go) stimuli. The latter four chords were the minor (C, E^{b}, G), sus4 (C, F, G), flat five (C, E, G^{b}) and augmented (C, E, $G^{\#}$) chords. Sounds were 76-82 dB in loudness as measured from the typical head position of a pigeon within the chamber (Radio Shack sound pressure meter; Weighting A, fast response). From previous auditory research (Heise, 1953; Kreithen & Quine, 1979) and our own (Cook & Brooks, 2009; Murphy & Cook, 2008), we knew that this volume and these frequencies were within their auditory range and capable of supporting auditory discriminations.

TRAINING

Each trial started with a peck to a centrally-located 2.5 cm white circular warning signal. This was replaced by a 6.7 cm purple square, to which the birds directed pecks during sound presentations. Each trial consisted of an 18.55 s sequence of presentations in which a single chord type was presented 12 times. Each individual presentation played for 1.5 s, interspersed by a 50 ms silent inter-stimulus interval (ISI); this was then repeated eleven times to make the whole sequence. Pecks directed towards the purple stimulus during the presentation of the C major chord on *go* trials (S+) were unpredictably reinforced with 2.5 s access to grain on a variable interval 8 s schedule (VI-8). During any within-trial reinforcements, the sound sequence continued to play. These go sequences also were reinforced at their completion. Pecks to no-go sequences (S–) were never reinforced and resulted in a dark time-out after the completion of the sequence that was proportional to the number of pecks emitted during the sequence (a 1 s penalty for each peck).

A small percentage (12.5%) of S+ sequences in each session were *probe trials* in which no reinforcement was given. These S+ probe trials allowed for the uncontaminated measurement of peck rate without the direct cues associated with any reinforcement on that trial and the missed time for pecking at the display that would have occurred while eating from the hopper during such trials. Only data from these probe trials were analyzed to estimate peck rates on the positive trials. The primary measure used to evaluate performance in this task was discrimination ratio, DR; S+ pecks /(S+ pecks + S– pecks), in which higher values indicate better discrimination. Chance discrimination (equal pecks to all conditions) would equal a DR of .5.

Birds were tested individually in daily sessions that consisted of 64 randomly ordered trials. All trials were randomly reordered each session. Of these 64 trials, 32 were trials in which the C major chord (S+) was played. The remaining 32 trials were divided equally among the four S– chord types (minor, sus4, flat five, augmented), for a total of eight trials per S– chord type per session. Thus, sessions were counterbalanced for frequency of go and no-go trials and the frequency of each no-go trial type. Acquisition and discrimination were measured over fifty sessions of training.

Results

Over the fifty sessions of training, three pigeons successfully learned to discriminate among the five chord types. Two pigeons failed to discriminate the auditory stimuli and were later removed from the experiment. Figure 1 shows the combined DR over training for the three successful pigeons for the chord types having manipulations of the third interval compared to the chord types having manipulations of the fifth interval. This figure reveals that semitone manipulations of the fifth supported faster and better discrimination than did identical manipulations of the third.

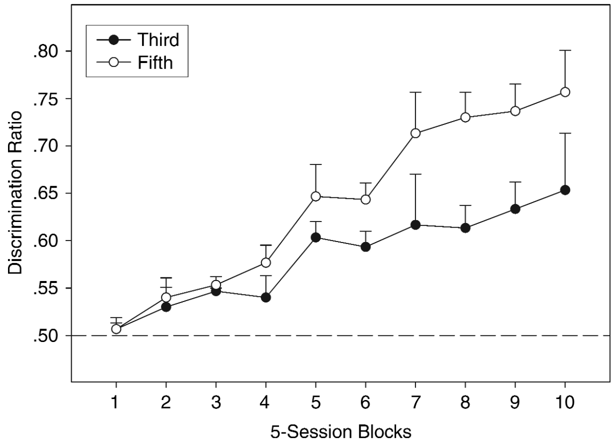

FIGURE 1. Mean discrimination ratio for the three successful pigeons over the fifty sessions of training for C-related chords with semitone manipulations of the third interval (minor and sus4) and fifth interval (augmented and flat five). The error bars represent the standard error of the mean.

To analyze these acquisition data, we conducted a repeated measures analysis of variance (ANOVA; 5-Session Blocks × 3rd vs 5th Chord Manipulation × Bird). The scores entered into this ANOVA were the discrimination ratios calculated for each S– chord type. This ANOVA revealed significant main effects of Blocks $F(9, 18) = 10.13$, $p < .001$, indicating that the birds improved as the experiment progressed, and Chord Manipulation, $F(1, 2) = 37.36$, $p < .001$, indicating that the birds were better overall at discriminating manipulations of the fifth interval in comparison to the third. There was also an interaction between Block and Chord Manipulation, $F(9, 18) = 7.62$, $p < .001$, indicating that the pigeons acquired the discrimination more rapidly for manipulations of the fifth.

Looking at the individual chords types during acquisition, the easiest chords to discriminate from the major chord were the augmented and the flat five chords. There was no statistical difference between these two chord types during initial training. For the two remaining chord types, the sus4 chord was the most difficult chord for the pigeons to discriminate differentiate from the major chord, while the minor chord was easier to discriminate from the major chord. These differences are detailed in the next section on steady state performance.

STEADY STATE

By the last two blocks of training, the rate of learning had slowed considerably. Thus, we used these sessions to judge how the pigeons were performing for each of the chord manipulations. At the end of this training for the three successful pigeons, the mean DR was .66

for the chords with manipulations of the third and .76 for manipulations of the fifth. For the four individual chord types, the mean DR was .77 for the augmented chord, .75 for the flat five chord, .70 for the minor chord, and .62 for the sus4 chord, with lower values indicating poorer discrimination from the major chord.

Besides analyzing performance on a between trial basis, we also examined discrimination across the multiple, repeated presentations of the chords that occurred within individual trials. This type of analysis has proven fruitful for examining other types of auditory discriminations using go/no-go tasks (Cook & Brooks, 2009; Murphy & Cook, 2008). The advantage of this kind of temporal analysis is its capacity to extract a continuous measure of similarity within a presentation. This is instructive because while the birds are inclined to peck vigorously at the start of all trials, as they accumulate information about the stimulus being presented, they can either keep pecking (on S+ trials) or withhold pecking (on S– trials). Thus, using this type of analysis, we can separate out pecks from early in the trial, when discrimination is relatively poor, from later in the trials when, if the birds can effectively discriminate the stimuli, they should have the greatest likelihood of inhibiting responding to the S– stimuli.

Using the last 10 sessions, the 12 repeated sound presentations from each trial were divided into groupings of three to examine performance as a function of serial position within the sequence. Figure 2 depicts the mean number of pecks for all three successful pigeons collectively and individually for each serial position grouping

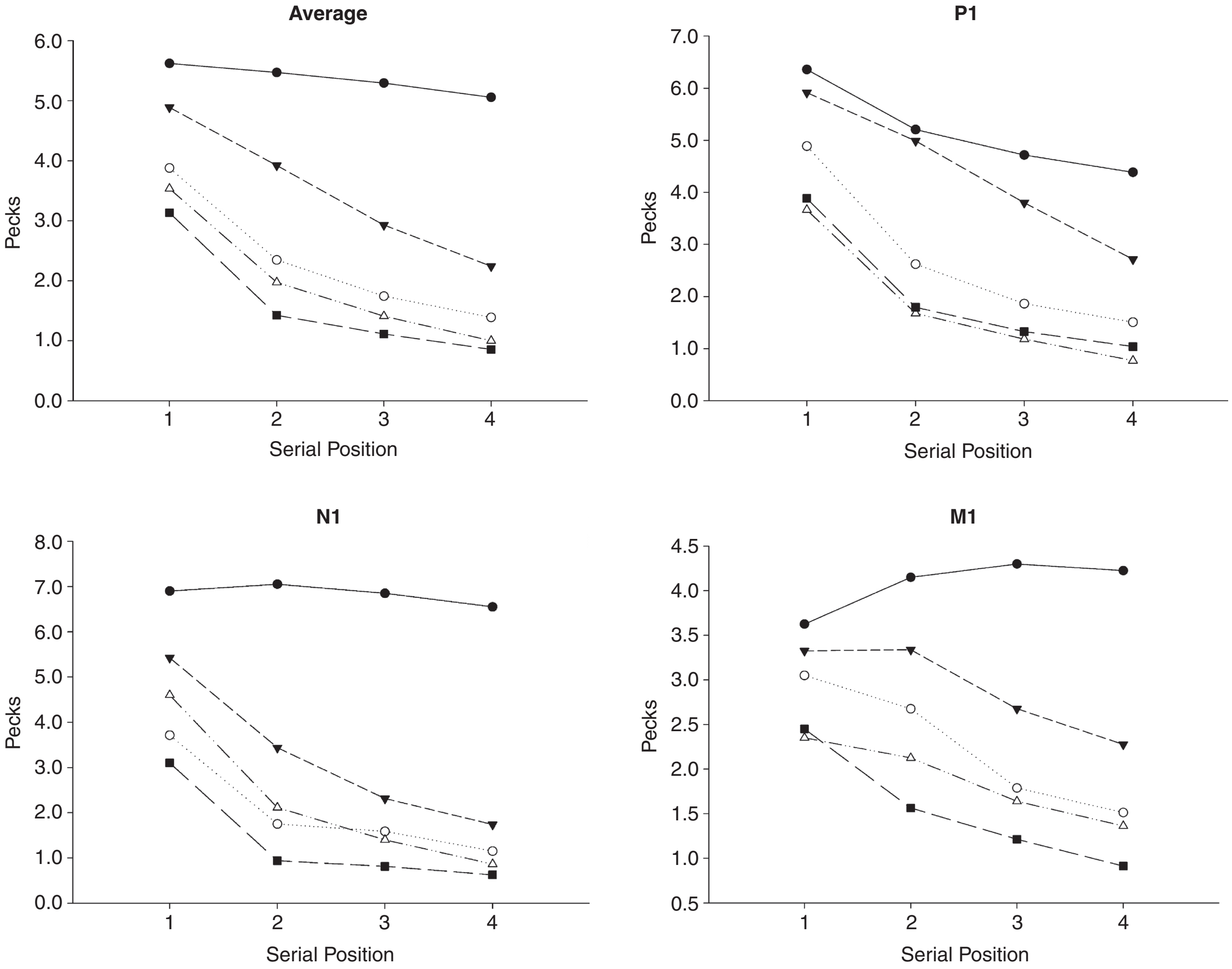

FIGURE 2. Mean peck rates for each C-related chord type as observed over the last ten sessions of Experiment 1. Serial position, as detailed in text, refers to three-item groupings within the twelve-sound presentation sequence that occurred on each trial.

TABLE 1. Mean Number of Pecks Emitted During Steady-State.

	Birds		
Experiment 1	P1	N1	M1
C Major	20.7	27.4	16.3
C Sus4	17.4	12.9	11.6
C Minor	10.9	8.2	9.0
C Flat 5	7.3	9.0	7.5
C Augmented	8.0	5.5	6.1

	Birds		
Experiment 2	P1	N1	M1
D Major	20.4	27.8	17.8
D Sus4	19.7	15.6	17.5
D Minor	19.9	21.3	16.7
D Flat 5	20.1	11.9	14.8
D Augmented	14.4	13.5	12.6
C Major	21.4	27.0	16.8
C Sus4	17.2	5.8	13.9
C Minor	14.3	4.8	9.4
C Flat 5	7.8	5.9	8.9
C Augmented	11.5	3.5	7.8

for the five chords tested. For each of the chord types, the pigeons discriminated with increasing accuracy over the course of an individual trial, as peck rates for the S+ and S– chords monotonically separated with repetition. For the most part, the pigeons improved their discrimination by withholding pecks to non-reinforced chords. Each pigeon clearly discriminated among the chord types by at least three presentations, as indicated by the separation in peck rates at the very beginning point of this figure.

This figure shows that all pigeons had a greater difficulty discriminating the sus4 chord from the major chord than any of the others, emitting the highest number of pecks early in the sequence and sustaining higher rates of responding to this chord type throughout the sequence. The mean peck rates for each chord type during this period can be found in Table 1. Paired *t*-tests between the total pecks emitted between all chord types during these last 10 sessions of training confirmed the increased likelihood of pecking to sus4 chords as compared to each of the different S– chord types for each bird [all $t(9)$s > 2.26, $p < .05$]. There was also an increased difficulty discriminating the minor chord relative to the other chord manipulations. Thus, while the sus4 chord was more difficult to discriminate, the minor chord was of medium difficulty. This same series of comparisons confirmed that each of the birds was able to quickly and significantly inhibit pecking to the augmented chord. For #N1, the augmented chord supported the best discrimination of all four S– chords [all $t(9)$s > 2.26, $p < .05$]. For the other two birds, the augmented chord was better discriminated than either the minor or sus4 chords, but not the flat five chord. The following is a summary of these *t*-test comparisons among cumulative peck rates for the individual birds for these ten sessions for all five chord types: #P1 major > sus4 > minor > flat five = augmented; #N1 major > sus4 > minor = flat five > augmented; #M1 major > sus4> minor > flat five = augmented.

Discussion

This experiment revealed for the first time that a non-songbird, the pigeon, was able to discriminate between triadic chords differing by only one semitone. The way in which the successful pigeons performed this discrimination indicated that they were sensitive to the interval relationships and complex harmonic content of these chord stimuli, often in ways similar to the human perception of these chord types. However, as in previous chord discrimination experiments with starlings and java sparrows, a minority of the pigeons did not successfully learn discriminate the stimuli.

The type of experimental design used to test the pigeons (go/no-go) produces peck rate data for both the S+ stimulus, during which the bird is supposed to peck, and the various S– stimuli, during which the bird is supposed to withhold pecking. Therefore, it is possible to use differential peck rates to the various S– stimuli to infer the perceived similarity to the major chord. The pigeons found the semitone manipulations of the fifth to be easier to discriminate than the same manipulation of the third. More specifically, each of the birds had the same general ordering of chord types, with the augmented chord being the easiest for all three birds, the sus4 being the most difficult, and the minor chord being discriminated with intermediate difficulty. The only difference in the three birds was that the flat five chord was of intermediate difficulty for one bird and much easier for the other two.

Two possible accounts can be given for the similarity with which the individual pigeons performed this discrimination. The first is that the pigeons processed the stimuli based on relational harmonic features, such as their overall sensory consonance and dissonance as first suggested by Hulse et al. (1995). If so, due to the highly consonant nature of the S+ major chord, we would expect that the pigeons should peck most strongly to the more consonant stimuli and peck less strongly to the less consonant stimuli. Indeed, the results appeared to confirm this possibility. The traditionally most consonant chords (sus4 and minor) were the most difficult for the birds to discriminate; the most dissonant (augmented and flat five) were the easiest. The role of triadic consonance and dissonance is discussed in more detail in the general discussion.

Absolute stimulus values, however, also may have influenced this discrimination in various ways. Although each S– chord shared two tones with the major chord, they also differed from it by a single tone. For example, the pigeons could have possibly processed the chords by attending to the different tones that distinguish the major chord from each S– chord rather than its overall harmonic configuration or tonal fusion. It is known that many birds, including pigeons, are highly sensitive to encoding and discriminating the absolute pitch of single tones (Friedrich, Zentall, & Weisman, 2007; Weisman, Njegovan, Williams, Cohen, & Sturdy, 2004). Despite the fact that this absolute feature was available for the pigeon to possibly use, it is unclear how appealing or workable such an account is in the current harmonic setting. For instance, it is not known if birds can even selectively attend to specific tones within harmonically complex triads that share common tones and higher harmonics. If the birds were so capable of selectively picking off the unique parts of the frequency spectrum, it is surprising that they also should have consistently greater difficulty discriminating those chords with manipulations of the third as opposed to manipulations of the fifth. It is perhaps possible that higher frequency tones are more salient or that tones within the middle of a triad are harder to detect, but why these might be case is not clear. While the processing of specific tones from within each chord seems unlikely to us, other types of absolute factors could have still played a role.

In both the visual (Gibson & Wasserman, 2003) and auditory (Murphy & Cook, 2008) modalities, absolute stimulus properties have been shown to play a role during the performance of relational discrimination tasks. Pigeons often are able to transfer relational discriminations to new stimuli, but in most cases they suffer generalization decrement during transfer, suggesting they had also memorized some of the absolute properties or configuration of the training stimuli. The influence of these absolute features is often exacerbated by using a small training set of stimuli in which few exemplars serve to accentuate the dimensional or categorical relations among the stimuli, and ameliorated by training with a larger set of stimuli (Katz, Wright, & Bodily, 2007; Wright & Katz, 2007). As our stimulus set was comprised of only five chords, the latter factor suggests that some memorization of the absolute harmonic configuration of the chords might have been possible.

Given the nature of our training procedure and the above considerations, we thought it likely that the pigeons had perhaps encoded relational and some absolute features of the stimuli, such as their overall sound quality The traditional and clearest test to evaluate the amount to which relational features impact a discrimination is to conduct a transfer test to new stimuli with similar relations, but with different absolute features. In the present case, that would be a new tonic root with chords comprised of the same interval structures. Due to the highly relational way in which humans process musical intervals, people regularly transpose chords and melodies to new tonic roots. In the next experiment, we examined how the pigeons would perform with the addition of a second set of chords organized around a different root.

Experiment 2

The main goal of Experiment 2 was to examine how chord discrimination shifted to a new tonal center. If the pigeons had only learned the general harmonic configuration of the chords, then they should easily transpose this discrimination to chords generated from a new root, or at least rapidly acquire this additional discrimination. To the extent that the learning of absolute features was involved, one would expect to see some degree of interference with either the transfer or subsequent learning of such new chords.

In this experiment, we added a second set of chords to the discrimination. These additional new chords were built from a D root. This root was chosen because the new and additional S+ major chord would share no tones in common with the previous C major chord. The pigeons experienced sessions in which half the trials were composed of the same five chords built on the C root as tested in Experiment 1 and the other half tested five structurally identical chords built on the D root. With both roots, the major continued to be the S+ stimulus and the four other chords types served as the S– stimuli.

Method

ANIMALS & APPARATUS

The three pigeons that successfully learned in Experiment 1 were tested. The apparatus was the same as in Experiment 1.

STIMULI

Stimuli were generated with the same method and materials as in Experiment 1. The new triads were composed of notes from the D major scale (D root note = 146.8 Hz). The D major chord (D, F#, A) was chosen as the reinforced stimulus. The four other chords again served as the non-reinforced (no-go) stimuli. These chords were the minor (D, F, A), sus4 (D, G, A), flat five (D, F#, A^b), and augmented (D, F#, A#) chords.

TRAINING

For two of the pigeons, these five D chord types were introduced as unreinforced probe tests before this test was began. The pigeons showed little pecking behavior to these stimuli during these tests. As a result, the pigeons were moved to a training procedure involving differential reinforcement to examine the acquisition with this new discrimination.

This training for all three pigeons was similar to Experiment 1, in that the major chord continued to serve as the S+, with all other chords serving as the S–. All sessions started with a block of 32 randomized discrimination trials using the chords made from the C tonality, with 16 S+ C major trials and 4 S– trials with the other four chord types. This was designed to sustain the previously acquired discrimination. This was followed by a block of trials testing the chords with D tonality using identical proportions of the five chord types. All of the birds had 64 scheduled D-related trials, though two of the birds (#P1 & #M1) had difficulty finishing sessions early in training. All experimental events were the same as in Experiment 1. Acquisition of the discrimination with these D-related chords was examined for 30 sessions.

Results

Shown in Figure 3 is the mean DR grouped into 5-session blocks for the semitone manipulations of the third and the fifth for D-related chords over the 30 sessions of Experiment 2. While performance with the C-related chords remained high during this period (see below), the pigeons struggled in learning to discriminate the new D-related chords. There was no evidence of any immediate transfer to the new D chords, as the pigeons discriminated at chance levels among all of these chords during the first session of their inclusion. During the first five sessions, some of the pigeons did show some relatively quick discrimination of the augmented and flat five chords, suggesting perhaps a small amount of savings, but otherwise there was little evidence of faster acquisition or savings.

A similar ANOVA (5-Session Blocks × 3rd vs. 5th Chord Manipulation x Bird) as used in Experiment 1 using the D-related chord data revealed no significant main effects of Block or a Block × Chord Manipulation interaction for DR, as the pigeons improved very little with training. There was a marginally significant trend of chord type, $F(1, 2) = 13.84$, $p = .065$, suggesting again that semitone manipulations around the fifth were easier to discriminate than around the third. This marginally significant effect of chord manipulation was due in part because of individual differences among the birds in their learning of the new chord types.

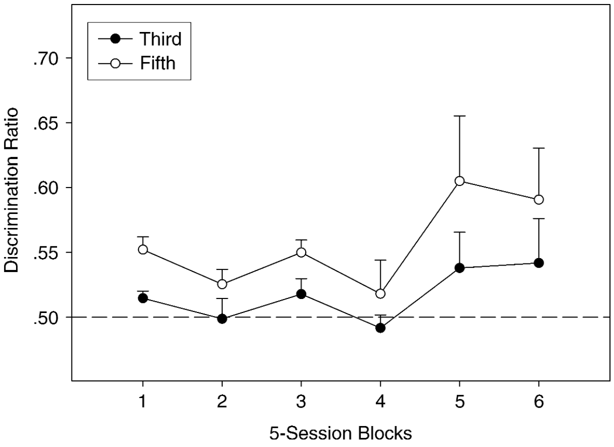

FIGURE 3. Mean discrimination ratio for the three pigeons tested in Experiment 2 over the thirty sessions of training for D-related chords with semitone manipulations of the third interval (minor and sus4) and fifth interval (augmented and flat five). The error bars represent the standard error of the mean.

STEADY STATE

Again, the last ten sessions of the experiment were used to evaluate relative performance with the individual chord types for each bird. Similar to Experiment 1, Figure 4 depicts the number of pecks emitted during each serial position grouping (three presentations each) for each of the chords tested for all three birds combined and for each pigeon individually. Although the birds had a harder time with these new chords in comparison to the well learned C-related chord, each bird learned some portion of the D-related chord discrimination.

The mean peck rates for each chord type can be found in Table 1. Bird #P1 learned the least, only discriminating the augmented chord from the D major chord. Paired *t*-tests with each of the chord types confirmed this difference, with only the augmented chord showing a significant difference in peck rate from the major chord [$t(9)\text{s} > 2.26$, $p < .05$]. Bird #M1 showed significant discriminations of both the flat five chord and the augmented chord from the major chord, but neither the minor or sus4 chords were found to be discriminated from the major chord for this bird. Bird #N1 was clearly the best of the three pigeons. Each of the four S– chords was significantly discriminated from the D major chord [all $t(9)\text{s} > 2.26$, $p < .05$]. In contrast to the first experiment, the minor chord supported the worst overall discrimination relative to the major chord,

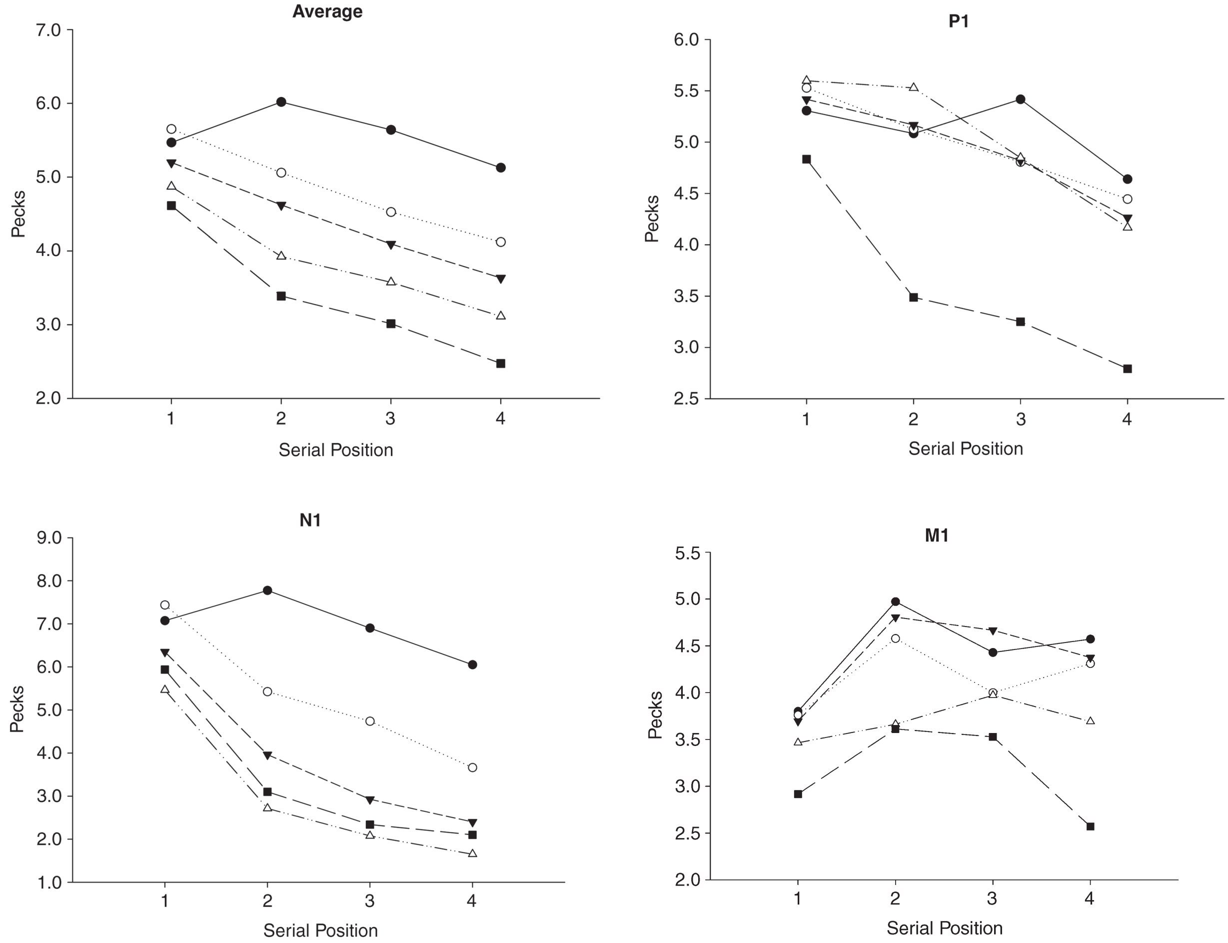

FIGURE 4. Mean peck rates for each D-related chord type as observed over the last ten sessions of Experiment 2. Serial position, as detailed in text, refers to three-item groupings within the twelve-sound presentation sequence that occurred on each trial.

while the flat five and the augmented chord were again discriminated best, and the sus4 chord fell in between. We found no significant differences between the sus4 chord and either the flat five chord or the augmented chord for this pigeon, although peck rates to this chord were consistently higher for this chord. The following is a summary of these *t*-test comparisons among peck rates for the individual birds across these ten sessions: #P1 major = sus4 = minor = flat five > augmented; #N1 major > minor > sus4 > flat five = augmented; #M1 major = sus4=minor > flat five > augmented.

Maintained discrimination of the C-related chords during these sessions was essentially the same as in Experiment 1. Mean DR over the last ten sessions showed the sus4 supported the worst performance (.63) followed by the minor chord (.69) and the flat five (.74) and augmented (.74) chords. Bird #P1 and #N1 showed highly similar patterns of chord discrimination as found in the first experiment, with the sus4 and minor chords supporting poorer discrimination from the C major chord relative to the augmented and flat five chords. Bird #M1 showed a seriously impaired discrimination of the sus4 chord relative to the other three chords, while all three of these chords were discriminated well and at an equivalent level. The following is a summary of the *t*-test comparisons among peck rates for the C-related chords during the last ten sessions: #P1 major > sus4 = minor > flat five = augmented; #N1 major > sus4 = minor > flat five = augmented; #M1 major = sus4 > minor = flat five = augmented.

Discussion

The first major result of Experiment 2 was that the pigeons showed no immediate transfer to the chords formed from the D root. While the pigeons may have perhaps showed some savings relative to the learning exhibited in Experiment 1 for the two easiest chords (augmented and flat five), it was clear that these new stimuli were also recognized as different from the previously experienced stimuli. Second, although not all of the birds fully learned all segments of this second discrimination, all of the birds were again much better able to discriminate the semitone manipulations of the fifth (augmented; flat five) than manipulations of the third (sus4; minor). This indicates that some of the same harmonic factors used to discriminate the C-related chords were perceived in the D-related chords, albeit perhaps with greater difficulty.

Overall, the learning of the additional D-related discrimination seemed hindered relative to the previously learned C chords. As discussed, this may reflect the fact that birds, in general, appear sensitive to item-specific, non-relational stimulus values in auditory stimuli. Weisman et al. (2004) proposed that birds and mammals may differ in their ability to use absolute and relational information within the auditory domain, especially with regard to their capacity to process the absolute value of pitch. They suggested that songbirds, and perhaps birds in general, are attuned to the absolute value of pitches, while mammals rely more on relational information within the auditory modality. Consistent with this hypothesis are a number of experiments showing that zebra finches, white-throated sparrows, budgerigars, and pigeons are very good to excellent at learning discriminations based on absolute pitch height, while humans and rats tested in identical procedures are generally poorer, especially in demanding situations that require precise segmentation of pitch range (Friedrich, et al., 2007; Weisman, et al., 2004). The latter may explain why humans are so flexible at transposing melodies, while in contrast, starlings, zebra finches, and pigeons seem constrained in their transfer of simple relational auditory discriminations, such as rising and falling pitch sequences (Cynx, 1995; Page, Hulse, & Cynx, 1989).

Thus, the poor transfer seen in Experiment 2 likely resulted from the pigeons memorizing the features of the C-related chords, such as their blended harmonic relations, the frequencies of the component pitches, or some combination of these features, and then recognizing that the new D-related chords differed in these properties. Thus, when presented with new pitches having the same harmonic structure or relations, their greater processing of these absolute qualities limited their performance and learning of these new chords based on their comparable harmonic structure.

Such attention to absolute factors may reflect that birds developed audition in a different evolutionary context than humans and other mammals. For instance, being able to detect the specific frequencies of songs in the environment might allow birds to identify either territorial intruders or conspecifics. For example, black-capped chickadee males shift their song's pitch to match that of nearby conspecifics while engaged in a territorial challenge, and females of this species use this cue to evaluate male fitness (Christie, Mennill & Ratcliffe, 2004). This same attentiveness to call pitch also was demonstrated in male nightingales, who modulated the pitch height of their whistle to match or exceed a call artificially produced by experimenters (Maguib, Mundry, Hultsch, & Todt, 2002). Thus, the perception and use of absolute pitch information may be critical to how many birds interact with conspecifics in both mating and aggressive contexts. Thus, while the pigeons were sensitive to harmonic factors as evidenced by their reactions to the different chord types in both experiments, continued training with a small stimulus set also may have impacted their ability to transfer their chord discrimination. Additionally, the continued and concurrent testing with C-related chords also may have interfered with their learning of the new D-related chords.

Despite the greater overall difficulty, all three pigeons learned all or a portion of the additional D-related discrimination. Further, the pattern of this discrimination shared many similarities with the first experiment. All birds discriminated the augmented chord best from the major chords, with the flat five being only slightly less discriminable. Both of these chords showed discrimination most rapidly and supported the best discrimination overall. The sus4 and minor chords were again the most difficult to discriminate from the major chord, with two pigeons exhibiting no discrimination for these chords involved the D-root. However, whereas the sus4 chord was clearly the most difficult to discriminate from the major chord involving the C root in Experiment 1, that pattern was not as clear in the second experiment. While this chord continued to be the most difficult for two birds, one bird showed no difference between the sus4 and the minor chord and more difficult discrimination of the minor chord with the D chords.

General Discussion

These experiments revealed four important new facets regarding auditory chord discrimination and perception by a non-songbird. First, the majority, but not all, of the pigeons tested were capable of discriminating these harmonically complex acoustic stimuli. Second, in both experiments, chords that had semitone manipulations of the interval based on the third (thus, having a preserved perfect fifth relative to the root) were perceived as more similar to the major chord than those chords in a similar manipulation around the interval of the fifth (thus, preserving the major third relative to the root). Overall, the pigeons found the augmented and flat five chords easier to discriminate from the major chord than the minor or sus4 chord. Third, the most difficult chord type for the pigeons to discriminate from the major chord was likely the sus4 chord, which was the slowest for them to learn and the most difficult for them to discriminate in the experiment with the best overall discrimination. Finally, we found little transfer or savings when we added a second set of chords built from a new root, suggesting the pigeons could not easily transpose this discrimination. While all three birds were able to discriminate the augmented and flat five chords from the major composed of this additional root, only one bird was able to discriminate all four chord types.

These data join those from starlings and java sparrows indicating that birds can discriminate triadic chords. Though one might otherwise assume that the perception of harmonic stimuli might require those biological mechanisms responsible for song learning, pigeons are classified as birds that do not learn their vocalizations and have limited neural connectivity involving in vocalization production (Emery & Clayton, 2005). The important addition of a non-songbird to this list of species capable of discriminating harmonic stimuli suggests that this discriminative capacity is not the result of a species-related acoustic discrimination such as song learning, but instead is likely widely shared across birds as a class.

It is interesting that despite being widespread in a comparative sense, Watanabe et al. (2005), Hulse et al. (1995), and our own study all report that a minority of the birds failed to learn their respective chord discriminations. Watanabe et al. (2005) reported that two of their six sparrows showed "unstable" responding, while Hulse et al. (1995) reported that two of their six starlings found chord discrimination too difficult. We similarly had two of our five pigeons not learn to perform the chord discrimination with C-related chords, and only one of the remaining three successfully learned to discriminate the entire set of D-related chords (although all three learned a portion of the latter). Thus, such harmonic discrimination appears not to be universal within a species. Whether these poorly performing birds may simply reflect individual variation within a species, some form of visual or attentional dominance, or some procedural limitation in each respective procedure is impossible to say. It is a curious state of comparative affairs, however, that some form of chord discrimination can be generally found across three very different species, but not universally across the individuals within them.

Both Hulse et al. (1995) and Watanabe et al. (2005) suggested that the consonance and dissonance of the intervals composing the different chords in their study may have provided the basis for their discrimination. Melodic (i.e., one note at a time) and harmonic (i.e., two or more notes at a time) consonance and dissonance are fundamental aspects of musical experience and appear to be mediated by several factors. The first involves the concept of sensory consonance. Sensory consonance is the idea that the ratios of the pitches comprising the component intervals are critical. Helmholtz (1885/1954) suggested that consonant intervals (e.g., octaves, perfect fifths) are the product of simple or small frequency ratios while dissonant intervals (e.g., minor seconds, major seventh) are composed of tones related by complex or large-integer ratios. While factors such as these may account for consonance in dyadic intervals, they may not completely account for human judgments of triadic harmony. Cook and his colleagues have suggested that an additional factor needs to be incorporated, a quality they have termed "tension," characterized by the equivalence of the intervals comprising a triad (Cook, Fujisawa, & Takami, 2004; Cook & Hayashi, 2008). Triadic chords composed of intervals of similar sizes are judged as more "tense" than those composed from component intervals of different sizes. The addition of this factor helps to account for human judgments of chordal consonance and dissonance. Finally, learned cultural factors and musical context also appears to influence the perception of consonance and dissonance of chords as individually dissonant chords and intervals can sound right within the right musical context.

Given human judgments of chord consonance (Roberts, 1986), two of our tested chords, the minor and sus4, are generally perceived as being more consonant and stable and having less tension than our augmented chord, which is judged as unstable and dissonant. Our flat five chord is a procedural creation of our experimental manipulation rather than a musical one, so previous judgments of it do not exist, but given its component tritone it is not surprising that it, too, sounds dissonant.

To provide a more direct comparison with the pigeons using exactly the same stimuli, we conducted some additional observations in which we asked eight human participants with little or no music training to explicitly judge the relative consonance and dissonance of our four S– chords relative to a C major chord. These participants were alternately played the major chord for two s, followed by a randomly selected augmented, flat five, minor, or sus4 chord for two s. After two presentations, they were asked to rate the "consonance" of the second stimulus on a 1 to 10 scale (with 10 being most consonant). Each participant judged each chord combination three times in a single session. When rank ordered, these participants found the sus4 chord (mean rating = 6.2) and minor chord (5.6) slightly more consonant to the major chord than either the augmented (4.3) or flat five (4.1) chords; *t*-tests of these ratings revealed no reliable differences between the sus4 and minor chord or between the augmented and flat five chords, but did confirm the differences between these two groupings.

To evaluate the similarity of human and pigeon results, we normalized the peck rate data obtained from the steady-state portion of Experiment 1 using the C root for each pigeon and similarly normalized the human ratings of the same chords. These normalized values were generated by computing *z*-scores for each of the similarity scores from each species. The results of this comparison are in Figure 5, which shows these adjusted scores for each chord type for each species. Overall, the pigeons and humans produced reasonably similar ratings for each chord type. Both pigeons and humans strongly agreed that the two manipulations of the fifth were most different from the major chord and agreed that the sus4 chord was numerically more similar to the major chord. The largest difference concerned the minor chord, for which pigeons produced a more intermediate ranking in comparison to humans, who found this chord generally consonant.

Though the humans tested in our study were not musicians, they assuredly brought a lifetime of exposure to Western music into the experiment, which likely strongly influenced their ratings. For example, humans were likely sensitive to the fact that some transitions (major-sus4-major) are relatively likely to occur in Western music, while other transitions are relatively rare (major-augmented-major). Thus, their ratings may reflect other factors besides the requested "consonance." Nevertheless, our human and pigeon results shared more similarities than not. Both pigeons and humans rated the augmented chord as highly dissimilar from the major chord, even though some theories based on sensory consonance suggest that it should appear consonant. One possibility is that both sensory consonance and triadic tension (Cook, et al., 2004;Cook & Hayashi, 2008) are factors in the perception of these chords by the pigeons. Along with triadic tension, a second explanation for the unexpected dissonance of the augmented chord can be found in a neurophysiological model of the temporal coding involved with tonal consonance (Cariani, 2004). This model, which has recently been applied to measure the consonance and dissonance of triadic chords (Cariani, 2009), also predicts a similar pattern of behavior as that observed in both pigeons and people. Specifically, this model predicts that major chords should be most consonant, followed closely by sus4 chords, and then minor chords. Augmented and diminished chords produce much more dissonant results (the flat five was not modeled in this analysis). Although our data do not disambiguate these (or other) possible explanations of triadic consonance and dissonance, they certainly attest to the generality of the phenomenon in the animal kingdom, and perhaps suggest that a comparative approach will be necessary for a fully parsimonious account of harmonic perception.

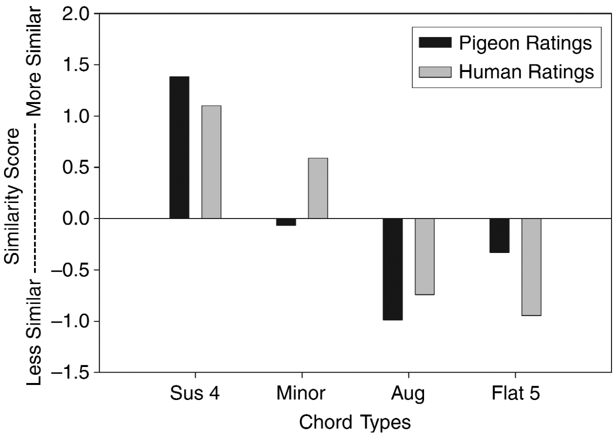

FIGURE 5. Normalized similarity scores for pigeons and humans for the C-related chords tested in Experiment 1 (see General Discussion for details).

It is important to note, however, that while the pigeons experience the harmonic relations of these frequencies in some ways similar to humans and some of the mechanisms involved may be similar, it does not mean that they experience them musically or affectively in the same way. Further experiments will need to look at how the relations between harmonic elements function together in such contexts in order to better evaluate that possibility. Nevertheless, the current results do suggest that such experiments are feasible and worth pursuing.

While the relative consonance and dissonance of the chords tested here provide an account of the discrimination of the different chord types, another notable feature of our data is that the pigeons did not readily transfer this discrimination to a new root. While all the birds were able to learn the apparently easier discrimination of the major from the dissonant chords, only one bird learned all chords types with both roots. Thus, while the pigeons may have been able to hear the consonant and dissonant harmonic relations within a set of chords, absolute stimulus factors likely interfered with using this same information with new sets of chords. It is also possible that the birds did not transfer simply because of the particular exemplars that were chosen as S+ and S– stimuli in this experiment. Future experiments using different stimuli, especially other chord types as the S+, or different procedures that emphasize greater relational responding, such as a successive matching or a same/different task, should provide important evidence related to understanding the failure to transfer in the current study.

Despite what appears to be increased attention towards and a general capacity for discriminating between absolute pitch by birds, many birds routinely produce relational pitch information in their song that is flexibly transposed across a relatively large frequency range. For example, the *fee* and *bee* sounds produced by the chickadee occur within a very precise interval ratio, dependent on the species. As might be expected given this flexible capacity for relational production, these birds also respond to interval information within conspecifics songs. However, it is important to note that these examples of relational pitch perception in the wild typically occur in sequential or melodic contexts rather than harmonic contexts, which may substantially alter the bird's ability to process these sounds relationally. Thus, transferring a harmonic chord discrimination may recruit different perceptual mechanisms than transferring between melodic arpeggios or scales.

Hulse et al. (1995) were finally able to eventually demonstrate that the starlings could transfer to new roots with their chords, but only after extended training with multiple new roots. The latter procedure may have caused their birds to shift from a greater attention to absolute factors to the use of the harmonic relations. When we subsequently compared our training regime to theirs, we may have been too impatient, as their starlings had not yet shown any savings at a comparable point within our experiments.

Given the apparent weight that absolute auditory features seem to have for birds, further research is needed to better understanding how such absolute and relational features compete for control both in the auditory and visual domain. Future researchers should pay greater attention to using procedures that promote relational control (e.g., use of many training exemplars) or prevent the use of absolute features (e.g., use of many roots) when interested in examining the perception of harmonic structure in animals. Even with such attention, the degree of weight given relational and absolute stimulus factors may be an important comparative difference between birds and humans, and may dramatically influence the appreciation of any harmonic "musical" experience by these animals.

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