

Mechanisms of Call Note-Type Perception in Black-Capped Chickadees (*Poecile atricapillus*): Peak Shift in a Note-Type Continuum

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We report on operant conditioning and artificial neural network (ANN) simulations aimed at further elucidating mechanisms of black-capped chickadee *chick-a-dee* call note category perception. Specifically, we tested for differences in the speed of acquisition among different discrimination tasks and, in two selected discrimination groups, searched for evidence of peak shift. Earlier, unreported ANN data were instrumental in providing the motivation for the current set of studies with chickadees and are provided here. The ANNs revealed differences in the speed of learning among note-type discrimination groups that is related to the degree of perceptual similarity among the three note types tested (i.e., A, B, and C notes). In many respects, bird and network results were in agreement (i.e., in the observation of peak shift in the same group), but they also differed in important ways (i.e., all discrimination groups showed differences in speed of learning in simulations but not in chickadees). We suggest that the start, peak and end frequency of the *chick-a* portion of *chick-a-dee* call notes, which form a graded but overlapping continuum, may drive the peak shift observed.

Keywords: peak shift, black-capped chickadee, acoustic discrimination, operant conditioning, artificial neural networks

Using songbirds as a model system to understand the cognitive and perceptual mechanisms (behavioral and neurobiological) that underlie communication allows us to bridge the gap between psychology and biology by investigating the mechanisms of learned behavior that play a pivotal role in an organisms' fitness. Here we focus on the perceptual mechanisms of one of the most

well-studied songbird species, the black-capped chickadee (*Poecile atricapillus*), and how they perceive call notes in their namesake *chick-a-dee* call.

The *chick-a-dee* call of the black-capped chickadee is composed of four note-types (A, B, C, and D; see Figure 1 for sound spectrograms of *chick-a-dee* call note types). The syntax of this call follows a strict ordering rule where $A \rightarrow B \rightarrow C \rightarrow D$ (Ficken, Ficken, & Witkin, 1978), and any note type may be repeated or omitted. Exceptions to this rule are rare (<1% of calls; Hailman, Ficken, & Ficken, 1985). These rules of syntax allow for "openness" in the number of call variants. That is, as the sample size of calls increases, new calls (differing in note-type composition) are observed.

The mechanisms of calls and call note perception have been uncovered in recent years through the use of field playback (e.g., Freeberg & Lucas, 2002), aviary playback (Templeton, Greene, & Davis, 2005), and laboratory-based operant conditioning experiments (e.g., Bloomfield, Farrell, & Sturdy, 2008; Charrier, Lee, Bloomfield, & Sturdy, 2005). For instance, in an operant GO/NO-GO paradigm, black-capped chickadees learned to discriminate *between* naturally occurring note-type categories faster than *within* note-type categories, suggesting that the note-type categories used by researchers to classify call components are also sorted into distinct, and similar, note-type categories by the chickadees that produce them (Sturdy, Phillmore, & Weisman, 2000). Sturdy et al. (2000) also demonstrated that adjacent note types on the continuum ($A \rightarrow B \rightarrow C$) were more perceptually similar than non-adjacent note types, thus squaring with earlier bioacoustical analyses (Hailman et al., 1985). Furthermore, black-capped chickadees also treat these note-type categories as open-ended; they can correctly classify novel note-type exemplars in an open-ended

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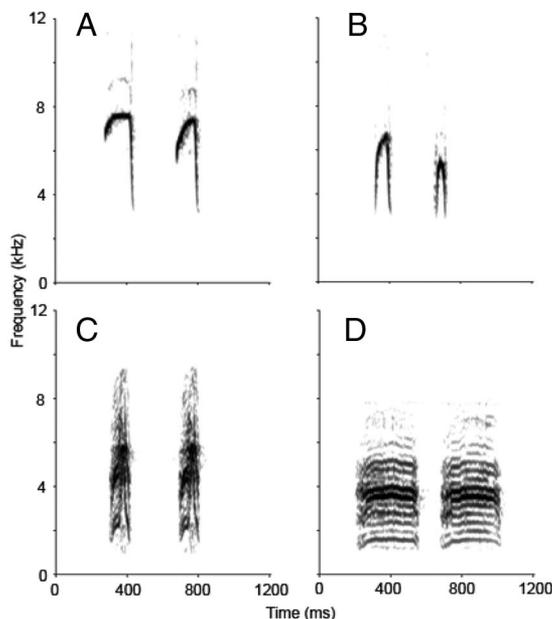


Figure 1. Sound spectrogram (transform length = 512 points) of the four component note types of the *chick-a-dee* call of the black-capped chickadee (A = A note, B = B note, C = C note, D = D note).

manner, rather than relying on rote memorization to solve the task (Charrier et al., 2005; Sturdy et al., 2000).

To elucidate which features of notes (i.e., temporal and spectral) governed note-type classification in black-capped chickadees; Charrier et al. (2005) devised an operant GO/NO-GO experiment in which the overall frequency of notes was shifted. When notes were linearly shifted in overall frequency, the birds' discrimination performance was altered. For example, if an S⁻ (unrewarded) note was shifted in frequency to be more similar to the S⁺ (rewarded) note, birds responded to the shifted S⁻ note as if it was an S⁺ note, and vice versa. These results suggest note frequency is a salient feature that chickadees utilize to classify note types. These results also provide further evidence (in addition to Sturdy et al., 2000, and Hailman et al., 1985) that note types in the *chick-a-dee* call form a perceptual continuum. The present study further explores this claim.

Nickerson, Bloomfield, Dawson, and Sturdy (2006) conducted parallel studies using perceptrons, simple artificial neural networks (ANNs) that were trained (i.e., that learned a discrimination task, not a data fitting model; see Dawson, 2004, for further details on the distinction), to discriminate note-types in the *chick-a-dee* call in a manner analogous to Charrier et al.'s (2005) original design. The ANNs produced many results that were qualitatively similar to the bird data. For instance, when the trained ANNs were probed with test notes shifted in frequency, network behavior was strongly and positively correlated with chickadee operant performance in that ANNs showed strong stimulus control by note pitch. In addition, when tested with nonshifted probe notes, ANNs showed appropriate generalization to these novel notes. It is interesting to note that ANN performance also revealed differences in the speed of acquisition among the different discrimination tasks not observed in the bird data. Specifically, A+B⁻/B+A⁻ discrimina-

tions required significantly more sweeps (i.e., training sessions) to reach training criterion than B+C⁻/C+B⁻ discriminations (referred to as AB and BC discriminations, respectively, hereafter). These differences in network performance arose, we surmised, due to higher perceptual similarity among A and B notes than among B and C notes. If this is the case, then we predict that discriminations involving note types that are even more perceptually distinct (i.e., A and C notes) would result in even faster acquisition than that observed in discriminations involving A and B notes or B and C notes for both birds and ANNs. In line with this prediction were simulation results unreported in the initial Nickerson et al. (2006) study. We found that, perceptrons learning A+C⁻ and A-C⁺ discriminations (referred to as the AC discrimination hereafter) reached training criterion the fastest of all discrimination groups; we provide this data in the results section of the current study. This data from the Nickerson et al. (2006) study was not initially reported due to the fact that we had no empirical bird data for comparison. These simulation results suggested that differences in perceptual similarity among note types were driving differences in speed of training observed in the ANNs.

Here we extend our exploration of note type categories by further testing the mechanisms of note-type perception in the *chick-a-dee* call of the black-capped chickadee. The present work used the same stimuli and similar training methods of Charrier et al. (2005), but differed in a few aspects. In the previous study, birds were trained *only* to discriminate adjacent (AB and BC) and not to discriminate nonadjacent (AC) note pairs. In the present study, birds were trained with all possible note combinations (i.e., AB, BC, AC) and were tested with novel A, B, and C notes, regardless of the note pair they were trained on. That is, birds trained to discriminate A and B notes would be tested with A, B, and C notes.

The aims of the current study are twofold. The first purpose was to extend the Charrier et al. (2005) chickadee experiment by adding the AC discrimination, thus training black-capped chickadees to discriminate among more combinations of note pairs (AB, BC, and AC) from their *chick-a-dee* call. This aim was inspired by the initial, unreported simulation findings discussed above, and reported in the results section below. This would allow us to compare empirical bird data to simulation results and to test for differences in perceptual similarity among note types. Such differences would be, we predicted, reflected in different rates of acquisition among different discrimination groups. If the *chick-a-dee* call does represent a natural perceptual continuum of note-type categories, then it should take the birds fewer trials to correctly discriminate nonadjacent note types (AC), compared to adjacent note-types (AB or BC). Our specific prediction, based on earlier modeling results, is that the AC discrimination would be learned the fastest by chickadees followed by BC and then AB discriminations. The second aim was to test for a positive peak shift in two discrimination groups (A-B⁺, B+C⁻), probing with note types not heard during initial discrimination training (i.e., probing with C notes following AB discrimination training). Early theories and empirical work with peak shift (e.g., Hanson, 1959; Spence, 1937) dealt with unimodal stimuli that were varied intradimensionally. More recent work (Spetch, Cheng, & Clifford, 2004) has demonstrated peak shift effects using multidimensional stimuli (e.g., upright and inverted human faces), which is more similar to the nature of our stimuli used for both birds (*chick-a-dee*

call notes) and networks (*chick-a-dee* call notes, represented as vectors of 9 features). If notes form not only a production but also a perceptual continuum, as was implied by the results of the earlier studies (e.g., Hailman et al., 1985; Charrier et al., 2005; Sturdy et al., 2000), then we would predict that peak responding during probe sessions would be observed to the untrained note-type that is furthest away from the S⁻ on the note type continuum. For example, birds trained in a B+C⁻ discrimination and then tested with untrained A notes should, according to this logic, show low levels of responding to C notes, high levels of responding to B notes (as the S⁺) and even higher responding to untrained A notes, thus demonstrating a form of peak shift (Hanson, 1959).

Method

Subjects

Twenty-four adult black-capped chickadees (*Poecile atricapillus*) were tested in 2007 and 2008. Nineteen of these birds were captured from sites around Edmonton, Alberta (53°30' N, 113°W) in 2006 and 2007. The remaining five birds were captured in Alberta at the Barrier Lake Field Station (51°02' N, 115°03' W) in 2004 and 2006. All birds were naive to experimental procedures. The sex of each bird was determined by DNA analysis.

Apparatus

A detailed description of the operant apparatus is provided in Sturdy and Weisman (2006). Briefly, each bird lived and worked in a modified cage (0.3 × 0.4 × 0.4 m). Each cage had several perches, water, grit cup and cuttle bone available. An opening in the cage (11 × 16 cm) allowed access to a motor driven feeder. Infrared cells monitored the opening to the feeder and a request perch that was situated in front of the feeder. The cage had a wire floor so birds could not recover spilled food. A Fostex FE108Σ speaker located on the outside of the cage broadcast acoustic stimuli. Each cage was housed in a ventilated, sound-attenuated chamber lit by a 9-W full spectrum fluorescent bulb. A single board computer controlled the experiment and monitored the response of each bird.

Acoustic Stimuli

Thirty notes from each of three notes-type categories (A, B, and C) were randomly selected from black-capped chickadee calls originating from Colorado, United States, and Ontario, Canada. Calls from different locations were equally represented across the three note types. See Charrier et al. (2005) for details of stimulus preparation.

Procedure

Nondifferential training. Nondifferential training ensures that all subjects hear and attend to all notes that will be presented during discrimination training. Each bird heard an equal number of notes (10 exemplars each of two note types) and was rewarded with access to food when it visited the feeder after each presentation. Nondifferential training continued until a bird visited the feeder on at least 60% of the trials for each note type for 6 bins of

500 trials (3,000 trials), with less than a 3% difference in response rates between the stimulus sets.

Discrimination training. Discrimination training began after completion of nondifferential training. Visits to the feeder following S⁺ notes were rewarded with access to food, while visits to the feeder after S⁻ notes resulted in no food access and a 30-s intertrial interval (ITI) with the chamber light off.

Response Measures

The percentage of response measure was calculated for each stimulus exemplar (S⁺ and S⁻) by dividing the number of trials on which the bird correctly visited the feeder by the total number of trials for that stimulus and then multiplying by 100. All response percentages were weighted according to number of times each exemplar was presented and corrected for zaps (trials where the bird left the perch before hearing the complete stimulus). The discrimination ratio (DR) was calculated by dividing the average percentage of response to S⁺ notes by the average percentage of response to all (both the S⁺ and S⁻) notes. Discrimination is at chance level when the ratio is 0.5 and perfect when the ratio is 1. Data were analyzed in bins of 500 trials.

Experiment 1: Note-type discrimination. Four different black-capped (2 male, 2 female) chickadees were assigned to each of six discrimination groups (A+B⁻, B+C⁻, A+C⁻, A-B⁺, B-C⁺, and A-C⁺). The note-type discrimination procedure consisted of three phases; (1) Acquisition, (2) Transfer 1, and (3) Transfer 2. In the Acquisition phase, each bird discriminated between two stimulus sets: 10 food-rewarded (S⁺) notes of one note-type category and 10 unrewarded (S⁻) notes of a different note type category (e.g., a bird in the A+B⁻ group would be rewarded for visiting the feeder after hearing one of 10 A notes, and punished by a 30-s ITI with the chamber light out for visiting the feeder after hearing one of 10 B notes). In Transfer 1 each bird discriminated between 10 novel exemplars from each stimulus set (10 novel S⁺ and 10 novel S⁻ notes). During Transfer 2 the stimulus sets from Acquisition and Transfer 1 were pooled so that the birds discriminated between the 20 S⁺ and 20 S⁻ stimuli previously presented. For each of the three phases, birds were trained until they performed six 500-trial bins with a DR ≥ 0.8, with the last two bins having occurred consecutively.

Experiment 2: Probe test. After completing Experiment 1 birds were probed with novel S⁺, novel S⁻, and exemplars from the untrained note-type category. In probe testing sessions S⁺ training stimuli were reinforced at 85%, S⁻ training stimuli were reinforced at 0% and all probe stimuli were reinforced at 15%. Probes testing sessions occurred on alternating days with regular discrimination training (Transfer 2 with S⁺ reinforced at 85% and S⁻ at 0%).

Network Architecture

The networks reported here used the same architecture and settings as those described by Nickerson et al. (2006). In brief, each network consisted of nine input units that were directly connected to one output unit (i.e., there were no "hidden" units), and was trained with the Rosenblatt program (Dawson, 2004). Each of the nine input units represented one feature of a *chick-a-dee* call note (start frequency, peak frequency, end frequency,

ascending duration, descending duration, total duration, frequency modulation in the ascending portion, frequency modulation in the descending portion, and the loudest frequency). These nine features have been used previously to classify note-types in the *chick-a-dee* call with 98% accuracy (Dawson, Charrier, & Sturdy, 2006). The output unit used a logistic equation (sigmoid-shaped) to convert the sum of the weighted signals from each input into an activity value that ranged between 0 and 1. The learning rate was set at 0.5 and training continued until the output unit produced an activity level of 0.9 or higher when the correct response to a pattern was to turn “on,” or produce an activity level of 0.1 or lower when the correct response was for a pattern to turn “off.” Each network served as one “subject” because prior to learning, the connection weights for each network were set to a random weight between -0.1 and 0.1 . Network responses were averaged over 10 “subjects” for each of the six discriminations.

Statistical Analyses

Independent t tests were conducted to test for differences in the number of bins (for birds) or sweeps (for ANNs) to criteria in different discrimination groups depending on which note type was rewarded. A one-way analysis of variance (ANOVA) was conducted to test for differential acquisition rates (number of bins or sweeps to criteria) among subjects in each of the three different discrimination groups and a repeated measures ANOVA was used to test for differences in responding (% response) between A, B, and C notes during probe sessions. Paired t tests were conducted to test for differences in DRs for all subjects between the last bin of Acquisition and the first bin of Transfer 1, and the last bin of Transfer 1 and the first bin of Transfer 2. All analyses were conducted in SPSS v 15 and Statistica v 8. All values are reported mean \pm 95% CI. We performed arcsine square root transforms on proportional data (% response, discrimination ratio) to determine the effects of nonnormality on p values on nontransformed data. Analysis of transformed data yielded the same significance levels; hence, we report the results of the analyses on untransformed data.

Results

There was no main effect for sex, $F(1, 18) = 0.003$, $p = .957$, or interaction between sex and discrimination group in the number of bins to reach discrimination criteria, $F(2, 18) = 0.121$, $p = .886$; therefore, we collapsed across sex for the remaining analyses.

Acquisition of Note Category Task

To determine whether birds learned the note-category task appropriately, we assessed performance across training stages of acquisition using paired t tests. There was no difference in DRs for all birds between the last bin of Acquisition (0.8796 ± 0.025) and the first bin of Transfer 1 (0.8579 ± 0.027 , $t(23) = 2.029$, $p = .054$) or between the last bin of Transfer 1 (0.9158 ± 0.019) and the first bin of Transfer 2 (0.9005 ± 0.027 , $t(23) = 1.461$, $p = .158$; see Figure 2). Because of the statistically marginal difference in DR for all of the birds between the last bin of acquisition and the first bin of Transfer 1, six additional paired t tests were conducted, one for each discrimination subgroup. For five of the subgroups there was no difference in DRs between the last bin of acquisition

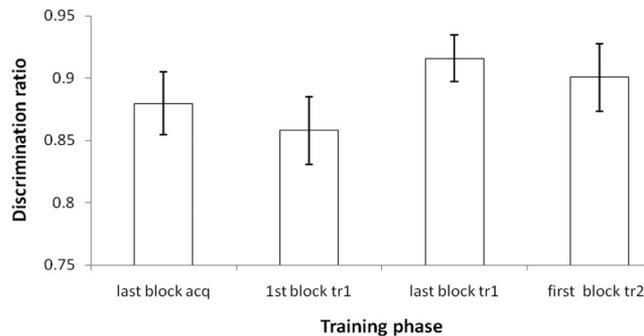


Figure 2. The mean \pm 95% confidence interval discrimination ratio for all subjects during different training phases (acq = Acquisition phase; tr1 = Transfer 1 phase; tr2 = Transfer 2 phase).

(A+B-, 0.84 ± 0.094 ; A-B+, 0.844 ± 0.041 ; B+C-, 0.90 ± 0.048 , B-C+, 0.873 ± 0.058 , and A-C+, 0.96 ± 0.025) and the first bin of Transfer 1 (A+B-, 0.84 ± 0.073 , $t(3) = 0.098$, $p = .928$; A-B+, 0.864 ± 0.083 , $t(3) = -0.594$, $p = .594$; B+C-, 0.85 ± 0.03 , $t(3) = 2.092$, $p = .128$; B-C+, 0.831 ± 0.083 , $t(3) = 1.267$, $p = .294$; and A-C+, 0.947 ± 0.015 , $t(3) = 0.754$, $p = .506$). The birds in the A+C- subgroup had significantly higher DRs in the last bin of acquisition (0.865 ± 0.041) compared to the first bin of Transfer 1 (0.821 ± 0.083 , $t(3) = 3.409$, $p = .042$). Even though the DRs were significantly lower at the start of Transfer 1, birds in the A+C- subgroup were still responding above the criterion ($DR \geq 0.80$). These findings indicated that in fact birds were responding to the discrimination contingencies appropriately both during initial acquisition and showed transfer (i.e., savings) when confronted with new, untrained exemplars of the same note types.

Acquisition Speed During Initial Discrimination

Independent groups t tests were used to determine whether differences existed between alternate versions of the discrimination task (e.g., between A+B- and A-B+ discrimination groups). There was no effect on acquisition speed (bins to criteria) according to which note in each discrimination was rewarded (A+B-, 34.25 ± 29.92 , A-B+, 24.25 ± 6.76 , $t(6) = 0.639$, $p = 0.546$; B+C-, 14.0 ± 3.49 , B-C+, 14.5 ± 4.96 , $t(6) = 0.162$, $p = .877$; A+C-, 16.0 ± 9.9 , A-C+, 8.75 ± 0.94 , $t(6) = 1.429$, $p = 0.247$). Therefore complimentary discrimination groups (e.g., A+B-, A-B+) were collapsed and analyzed as AB, BC, and AC for further analyses unless otherwise stated. We collapsed across reciprocal discriminations (e.g., A+B-, A-B+) because we were concerned with the birds' ability to discriminate between adjacent note-types (e.g., A and B, and B and C notes) and nonadjacent note types (e.g., A and C notes).

A one-way ANOVA revealed that there was a significant difference in the number of bins to criteria for initial acquisition among the three different discrimination groups, $F(2, 21) = 3.917$, $p = .036$, $\eta_p^2 = 0.272$. Tukey post hoc comparisons revealed that subjects in the AC discrimination group learned the initial acquisition in significantly fewer trials (12.375 ± 6.43) than subjects in the AB discrimination group (29.50 ± 17.71 , $p = 0.047$), but not in significantly less trials than subjects in the BC discrimination

group (14.25 ± 3.4 , $p = 0.957$). There was no significant difference in responding between subjects in the AB and BC discrimination groups, $p = .083$.

Independent groups t tests were also used to determine whether differences existed between alternate versions of a discrimination task for the ANNs. There was no effect on acquisition speed (sweeps to criteria) according to which note in each discrimination group was rewarded (A+B−, 638.9 ± 0.616 , A−B+, 639.1 ± 0.542 , $t(18) = 0.477$, $p = 0.639$; B+C−, 259.3 ± 3.96 , B−C+, 259.4 ± 4.3 , $t(18) = 0.034$, $p = .974$; A+C−, 32.1 ± 0.2 , A−C+, 32.1 ± 0.46 , $t(18) = 0.0$, $p = 1.0$). Therefore complementary discrimination groups (e.g., A+B, A−B+) were collapsed and analyzed as AB, BC, and AC unless otherwise stated.

A one-way ANOVA revealed that there was a significant difference in the number of sweeps to criteria among the three different discrimination groups, $F(2, 57) = 130651$, $p < .001$, $\eta_p^2 = 1$. Tukey post hoc comparisons revealed that networks in the AC discrimination group reached criteria in significantly fewer sweeps (31.0 ± 1.7) than networks in the AB (639.0 ± 1.7) or BC (259.35 ± 1.7) discrimination groups ($p < .001$ for both). Networks in the BC discrimination group reached criteria in significantly fewer sweeps than networks in the AB discrimination group, $p < .001$.

Peak Shift in Note-Type Continuum

To determine whether birds in the A−B+ and B+C− group exhibited peak shift, we compared percentages of response to probe notes from all three note types (A, B, C) using repeated measures ANOVAs followed by Tukey post hoc comparisons. Birds in the A−B+ group responded differentially to A (20.8 ± 30.9), B (54.2 ± 40.8), and C (91.7 ± 16.3 , see Figure 3) probe notes, $F(2, 6) = 9.169$, $p < .01$, $\eta_p^2 = 0.753$. Tukey post hoc comparisons revealed that birds responded significantly more to C notes than to A notes, $p = .012$. Birds' response to B notes did not differ from A notes ($p = 0.19$) or C notes ($p = 0.138$). Networks trained in the in the A−B+ group responded differentially to A (2.2 ± 0.01), B (88.4 ± 0.045), and C ($100.0 \pm 1.26E-7$) probe notes, $F(2, 18) = 17159473.0$, $p < .001$, $\eta_p^2 = 0.99$. Tukey post hoc analyses revealed that the networks responded significantly more to C notes than B notes ($p < 0.001$) or A notes ($p < .001$). Networks also responded significantly more to the B notes than to the A notes ($p < 0.001$).

Birds in the B+C− group responded differentially to A (79.2 ± 20.6), B (87.5 ± 15.6) and C (12.5 ± 8.2) probe notes, $F(2, 6) = 19.909$, $p = 0.002$, $\eta_p^2 = 0.87$. Tukey post hoc comparisons revealed that birds responded significantly more to A and B notes than compared to C notes ($p = 0.005$, 0.003 , respectively). There was no difference in the birds' response levels to A and B notes, $p = 0.804$. Networks trained in the B+C− group responded differentially to A (73.0 ± 0.1), B (78.0 ± 0.03), and C (0.0 ± 0.0) probe notes, $F(2, 18) = 2283944$, $p < .001$, $\eta_p^2 = 0.99$. Tukey post hoc comparisons revealed that networks responded significantly more to B notes than C notes ($p < .001$) or A notes ($p < .001$). Networks also responded significantly more to A notes than C notes ($p < .001$).

Discussion

Here we expanded on Charrier et al. (2005) where we examined the mechanisms underlying note-type classification in the *chick-*

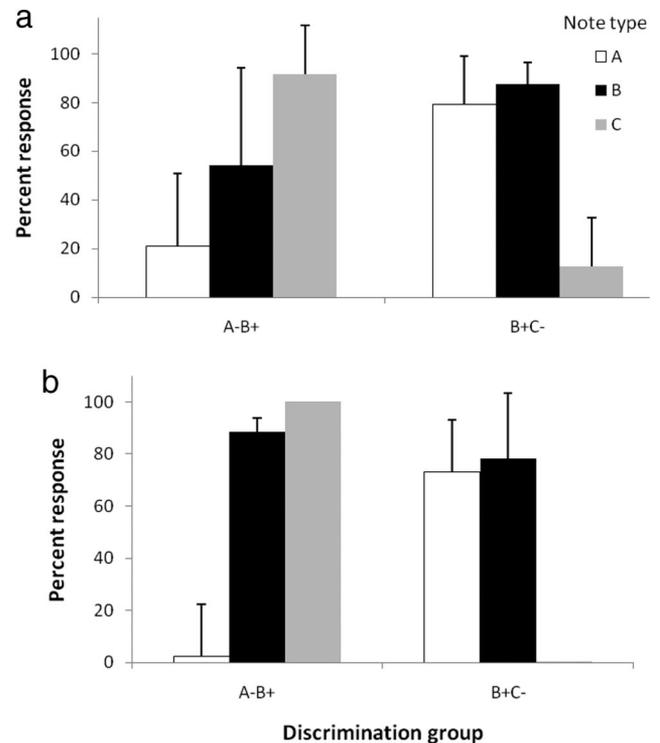


Figure 3. The mean \pm 95% confidence interval percent response to A (white bar), B (black bar), and C (gray bar) probe note presentations for subjects in the A−B+ and B+C− discrimination subgroups, panel a is data obtained from chickadees and panel b is data obtained from Artificial Neural Networks.

a-dee call of the black-capped chickadee. We report additional, previously unpublished data from Nickerson et al. (2006). These ANN data inspired the analogous training and testing of black-capped chickadees presented, along with the ANN data, in the current study. In both the ANN and chickadee data we tested for evidence of differences in speed of acquisition among discrimination groups (in ANNs where there is no inherent biological relevance or experiential components, and in chickadees where there is) and also test for evidence of peak shift in two selected groups.

We found evidence for open-ended classification of note-types, in agreement with past research (e.g., Sturdy et al., 1999; Charrier et al., 2005) in two ways. Birds in all subgroups demonstrated savings across the different stages of acquisition training and, for the B+C− subgroup, continued to correctly classify note-types when they were presented with novel exemplars of each note-type during probe testing. This pattern was also observed for both A−B+ and B+C− subgroups in the ANNs when they were presented with novel S+ and S− notes during probe testing in that the networks continued to correctly discriminate between novel S+ and S− exemplars.

The birds, like the ANNs, differed in the number of trials required to learn the different discrimination tasks and this varied contingent on the note-types they were required to discriminate between. The ANNs learned the AC discrimination fastest (i.e., in the least amount of sweeps) with the BC discrimination learned next fastest and the AB discrimination taking the longest to learn.

In a similar manner, the birds also learned the AC discrimination faster (i.e., the least amount of trials) than the AB discrimination, but not faster than the BC discrimination. However, unlike the ANNs, the number of trials chickadees needed to reach criteria for the BC discrimination was not significantly different than either AB or AC discriminations. The pattern of results observed in chickadees suggested that it is easier to discriminate between nonadjacent note types (AC) compared to one adjacent note-type pair (AB) but not another adjacent note-type pair (BC) on the production/perception continuum of the *chick-a-dee* call (Hailman et al., 1985; Sturdy et al., 2000). Based on the results of the ANN we also predicted that it would take fewer trials to reach criteria for the BC discrimination compared to the AB discrimination. This was in part because AB notes appear more similar when viewed on a sound spectrogram, in that both A and B notes are tonal in nature, rising, peaking, and then decreasing in frequency. C notes, on the other hand, are markedly different; they have rapid ascending and descending frequency modulation accompanied by harmonic or harmonic-like bands (Ficken et al., 1978; Charrier, Bloomfield & Sturdy, 2004). However, because the BC discrimination appeared to be intermediary to AB and AC discriminations (not significantly different from either while AB and AC were significantly different from each other), we take this as evidence that A and B notes, and B and C notes, share more similarities in perceptual (multidimensional) space, than A and C notes.

Probe testing the birds and ANNs with “off category” A, B or C notes allowed us to test for presence of the positive peak shift phenomenon (Guttman, 1965) in two discrimination groups: A–B+ and B+C–. Following previous studies (Sturdy et al., 2000; Charrier et al., 2005) that suggest the note types that make up the *chick-a-dee* call of the black-capped chickadee form both a production and perception continuum with strict syntax (Hailman et al., 1985), we expected that when tested with all three note types, the birds and networks would respond more to the untrained note-type, compared to the S+ note-type, due to an interaction of the underlying excitatory and inhibitory gradients formed around the S+ and S–, respectively.

The birds demonstrated peak shift (Hanson, 1959; Spetch et al., 2004) in the A–B+ but not the B+C– discrimination group. In the latter group, birds still responded significantly more to the untrained note-type than the S– note-type, but the responding to the untrained note-type was not significantly different (i.e., not greater) than the response to the S+ note-type and therefore no peak shift was observed. Similar to the birds, the ANNs demonstrated peak shift in the A–B+, but not the B+C– discrimination group. ANNs in the latter group responded more to S+ note-types than either S– or untrained note-types, however, the networks also responded more to the untrained note-types, compared to the S– note-types.

Why peak shift is witnessed in one discrimination group but not the other is unclear. In the A–B+ discrimination group, the peak in responding shifted from the previously trained S+ (B notes) to the previously untrained C notes. In the B+C– group, a peak shift response was not witnessed, and the birds and networks continued to respond to the previously trained S+ (B notes) at high levels, while also responding at high levels to the untrained A notes. The lack of a peak shift in the latter group could be interpreted as an area shift (Rilling, 1977), since the birds and networks were responding at levels higher than chance to the untrained A probe notes. An area

shift is also possible if the birds are treating the untrained A notes as part of the same category as B notes, because of their higher degree of perceptual similarity (i.e., A and B notes are both tonal notes whereas C notes are harmonic notes). However, more extensive pretraining with additional note types from the *chick-a-dee* call that are all initially nondifferentially reinforced is needed to confirm and/or differentiate the presence of a peak and/or area shift in this group.

Nonetheless, we take this data as preliminary evidence of the peak shift in multidimensional acoustic stimuli, that is, the naturally occurring note-types within a *chick-a-dee* call. Previous bioacoustic research examining the notes of the *chick-a-dee* call (Charrier et al., 2004) and the mechanisms of note-type perception with chickadees and ANNs lead us to suggest that the frequency of call notes defines the continuum which underlies the behavior of the birds and networks in the current study.

Figure 4 shows the average frequency (in hertz \pm one standard deviation) of the A, B, and C notes of the *chick-a-dee* call in three panels, one for each frequency measure (start, peak, and end frequency; Charrier et al., 2004). In examining each panel separately, it is clear that the mean start, peak, and end frequencies for A notes are higher than B notes, followed by C notes. It has also been demonstrated that birds misclassify A, B, and C notes in operant discrimination tasks as the frequency of these note types are shifted up or down, while the duration measures are held constant (Charrier et al., 2005).

Examining the start frequency of A, B, and C notes (panel a, Figure 4) we observe that the average start frequency of B notes is closer to the average start frequency of C notes, compared to A notes. This suggests that a strong positive peak shift should be witnessed in the B+C– group because of the small relatively small difference between the S+ (B notes) and S– (C notes). However, peak shift is not witnessed in this discrimination, but peak shift is witnessed in the A–B+ discrimination, where the S+ and S– are relatively further away from each other (one and a half times away, compared to B and C notes). These findings are counterintuitive when considered in light of unimodal stimulus

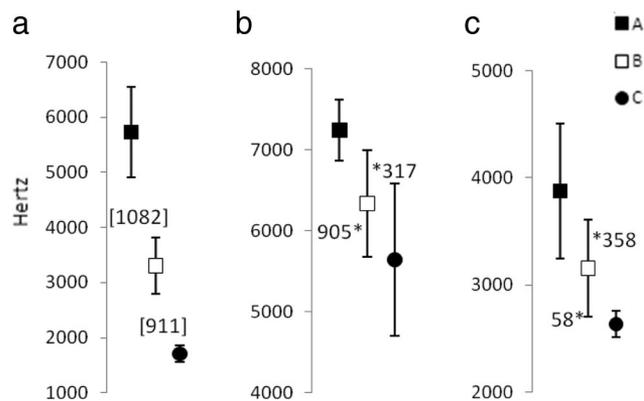


Figure 4. The (a) average start frequency, (b) peak frequency, and (c) end frequency for A (filled squares), B (open squares), and C notes (filled circles) \pm one SD (Charrier et al., 2004). The numbers in brackets in panel a represent the difference in hertz between adjacent note types. The asterisked numbers in (A) and (B) represent the overlap in hertz between adjacent note types.

tests of peak shift (e.g., Hanson, 1959) but we feel are likely because of the multimodal nature of our stimulus pool.

Furthermore, this apparently straightforward frequency continuum is complicated by the fact that A and B notes have a greater variability in start frequency, compared to C notes. From panel a of Figure 4 we see that distance separating the lower limits of the start frequency of A notes (one standard deviation) from upper limits of B notes (one SD) is 1,082 Hz (the bracketed number) is similar to the distance separating the lower limits of the start frequency of B notes from the upper limits of the start frequency of C notes, 911 Hz. Figure 4 (b) and (c) are different from (a), and similar to each other in that there is much overlap in the average ranges for the peak, and end frequencies of A, B, and C notes. While there is a greater overlap between B and C notes for peak frequency (905 Hz, signified with an asterisk) compared the overlap between A and B notes (317 Hz). The opposite pattern is true for the end frequency, where the A and B notes overlap by 358 Hz, compared to an overlap of 58 Hz between B and C notes. Our goal of the preceding paragraphs is to suggest that while the frequency of *chick-a-dee* call notes forms an absolute graded continuum, there is much featural overlap, resulting in complex, multidimensional acoustic stimuli. Furthermore, we suggest that this frequency continuum is mediating the birds and networks' responses in the current study.

This idea that certain features of multidimensional stimuli can mediate a peak shift or area shift effect is consistent with data reported by Spetch et al. (2004). In their study, human faces were morphed with a computer program to range from "unique" to "average". Spetch et al. found a similar peak shift effect for human subjects using both upright and inverted faces. This finding (i.e., peak shift with inverted faces) supports the notion that humans were using featural information to solve this task rather than using configural, in processing the multidimensional stimuli. Our findings here are in line with this.

We suggest that future research aimed at elucidating peak shift in a note-type continuum should involve operant conditioning discriminations and artificial neural networks using all four note types (A, B, C, and D) present in the *chick-a-dee* call as discriminative stimuli. This would better enable us to test for peak shift and to do so in a more comprehensive, biologically relevant manner. Furthermore, it would be informative to increase the number of note types used in these tasks to determine the effects that expanded stimulus ranges have on the observation of peak shift. In each of these cases, conducting parallel studies using chickadees and ANNs would allow us to explore and sort out the possible role that experience (i.e., that the birds necessarily bring into the task and the ANNs do not) has on the observation, or lack thereof, of peak shift in a multimodal, biologically relevant, note type continuum.

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