

An Examination of Stimulus Repetition in Complex Sounds in a
Same/Different Discrimination by Pigeons (*Columba livia*)

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Abstract

In practically every animal that uses the auditory modality, distinguishing between complex sounds is a constantly occurring and extremely important process. Complex sounds are sounds that differ continuously over the course of their duration. In animals such as songbirds, this processing is paramount to understanding the calls of their conspecifics. This study examines recent data using procedures originally by Cook and Brooks (2009) to test for complex sound processing in pigeons, vocal nonlearners with no capacity for song. Four pigeons (*Columbia livia*) were trained in a go/no-go task in which they successfully learned to peck at sequences of different sounds and withhold pecking during same-sound sequences of complex stimuli. Repetitive (same) trials were analyzed to see what factors influenced the birds pecking. The study found that pigeons suppressed pecking more on birdsong stimuli versus artificial complex sounds and largely ignored local patterns in sound, ostensibly demonstrating that pigeons too demonstrated a holistic ability to integrate sounds over time into comparable units.

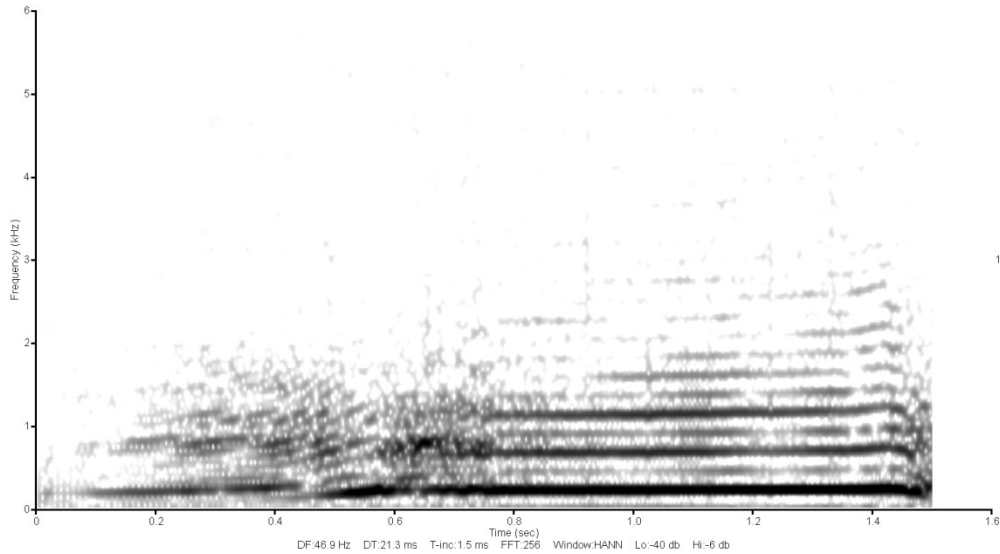
Introduction

The ability to recognize similarity across sounds and organize them into groups is an important yet poorly understood aspect of auditory perception. Most do not spend a great deal of time wondering why two quacks from a duck sound the same, yet each quack contains a broad range of information that differs greatly over time; the brain somehow accomplishes the daunting task of gathering this chaotic flow into a distinct group from which it can form comparisons with other sounds. Though a great deal of resources have been devoted to the organization of sound into units in humans, especially in parsing language, this same perceptual ability for other sounds in non-human animals has been largely ignored despite the information on general audition and auditory cognition that could be potentially gleaned from such studies. Animals must discriminate between noises in which pitch and loudness shift over time, yet many can and must recognize when these constant varying sounds are similar to each other.

The wide range of information which sound can contain will be discussed, ranging from absolute, lower-order properties, such as frequency and amplitude, to higher-order properties such as repeating units, contours, and the presence of harmonics. This includes an introduction to the spectrogram, a representation of sound widely used for acoustic analysis and comparison. Previous literature on how animals' comparison between these properties may confer advantages will be examined, revealing the ethological significance of this psychology mechanism. Finally, an experiment by Cook and Brooks (2009) testing the ability of pigeons (*Columba livia*) to perform discrimination among complex sounds, its significance for our current understanding of birdsong and complex sound discrimination, and how the current study builds off its results will be explained in detail.

As one must understand light to study vision, it is first necessary to become familiar with the structure of sound to realize why the auditory processing of complex sounds warrants such a great deal of investigation. Much like vision, very often the information provided to the auditory system largely consists of a wide scattering of excitation by waves. As longitudinal waves, sound waves represent varying levels of pressure that differ from each other only in amplitude and frequency; these waves may summate into more complex forms from as early as their source and can encounter numerous sources of distortion and degradation before they ever reach the listener. Any system of perception attempting to make sense of sound must first deal with this raw data and somehow accomplish the convoluted task of resolving the turbulent information into auditory and psychological units that must be detected, discriminated among, and integrated over time. The temporal component of sound makes it different from other modalities and is extremely significant in regard to audition. It must be taken into account whenever analyzing sound that all information is presented as in a manner akin to a scene in which time composes a dimension.

To quantify this complicated array, thorough mode by which to yield information about sound is necessary. One method of looking at sound that proves useful for analysis is called the spectrogram (Figure 1). The modern spectrogram represents a short-time Fourier transform, a mathematical representation of an observed waveform as a series of sinusoidal waves, each with its own frequency and amplitude. Resolving the sound in this fashion transforms the waveform into a series of columns for extremely small time intervals; within each column is a measurement



of amplitude versus frequency at each point in time. The final result is a function of frequency over time in which the cells have varying shades of color or darkness to represent the relative intensities of each frequency.

When looking at individual sounds, the spectrogram provides numerous advantages. As a result of the native waveform being pulled apart, the three chief dimensions of amplitude, frequency, and time that comprise a sound may be calculated from it. Whereas the native waveform varies in the spacing and prominence of its peaks, the spectrogram has already “carved” the wave data into a series of columns with discrete values. This allows both basic operations, such as mean frequency or amplitude over time, to be calculated, as well as allowing more context-specific analyses such as setting a minimum loudness for an average frequency calculation. Furthermore, the spectrogram presents a more intuitive image of sound to the naked eye and may reveal patterns not immediately audible; a glance is often sufficient to give a gross estimate of a sound’s properties. For example, the harmonic rising and falling of the wood

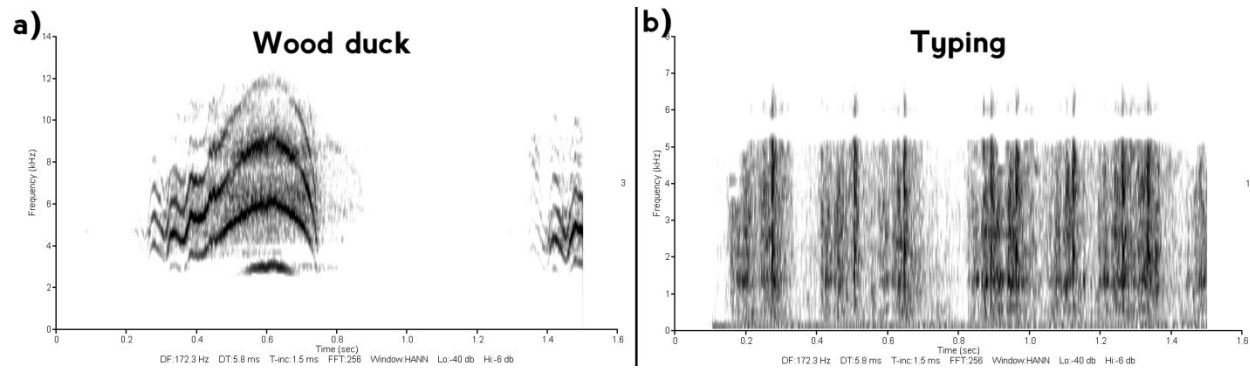


Fig. 2. SIGNAL output of the spectrograms of wood duck, a bird call, and the sound of someone typing on a computer keyboard. The former demonstrates the discrete frequency contours reminiscent of bird calls while the latter represents the low-frequency, unfocused pattern characteristic of environmental noise.

duck's call is visible in the dark bands of its spectrogram, whereas a sound that repeats but has no discernible pitch, such as typing on a keyboard, has these qualities reflected in its spectrogram (Figure 2). Through cursory visual inspection and in-depth auditory analysis, the spectrogram's main utility lies in that it opens the door to fully exploring a sound.

Characteristics such as frequency and amplitude, wave properties that correspond to pitch and loudness when perceived in sound, comprise what are here termed lower-order features. Thus, lower-order auditory perception refers to the act of picking up absolute values of these properties or averages across the course of a sound. To discriminate between two different sounds using such lower-order statistics, one must simply compare the difference in values of these simple characteristics between them.

As might be expected, low-order sound comparisons can be found widespread among perception of animals. Many animals, especially birds, attend to the chief frequency of a sound to compare and contrast the information it presents. Mager, Walcott, & Piper (2007) traced the dominant frequency in the call of the male common loon (*Gavia immer*) and found it to correlate inversely with body mass and general condition. A similar correlation was found between call frequency and body size in male little penguins (*Eudyptula minor*), and playback of low-

frequency calls by male little penguins to females elicited more responses than high-frequency calls (Miyazaki & Waas, 2003). Perhaps unsurprisingly, amplitude differences between sounds have been found to be used by humans (Mershon & Edward, 1975) and singing birds such as the eastern towhee (*Pipilo erythrophthalmus*) (Nelson, 2000) as one of several factors in judging the relative distance of a sound.

Higher-order characteristics draw upon the absolute components of a sound but construct groupings and relations over time between different areas of the sound. One example of a more integrative measure by which animals may extract information is the number of repetitions in the calls they generate and hear. As a higher-order characteristic, repetition is independent of the absolute content of each constituent and instead relies on the perceiver recognizing a pattern of similarity and organizing the recurring sound into countable units. Dolphins have been demonstrated in captivity to repeat ultrasonic clicks at slow intervals in what has been deemed a “train” of clicks (Lilly & Miller, 1961). Higher rates of repetition have been shown to precede the performance of specific behaviors such as leaping maneuvers in Hector’s dolphin (*Cephalorhynchus hectori*) (Dawson, 1991), suggesting repetition may play an important role in communication. Sperm whales, another cetacean, have been hypothesized to use the rate at which they emit their own ultrasonic clicks as an indicator of age (André & Kamminga, 2000).

Oscine (singing) birds present perhaps the most salient example of the use of repetition in auditory production and recognition. In birdsong, the presence of complex higher order repeating units known as syllables defines one example of repetition’s significance in animal calls. Similar to how notes may compose a musical piece, syllables are the individual auditory units that form birdsong and are formed from distinct, almost pure-tone frequency bands (Lemon, 1997). Just as the repetition of other species’ calls yields useful information, the ability

to retain and relate syllables of birdsong back to previous utterances allows oscine perceivers to gauge the traits of the caller. Wildenthal (1965) noted that this repetition of units can form groups on multiple levels and speculated that the number of repeating units helps mockingbirds differentiate each other from similar mimics such as the Brown Thrasher; variation within patterns in turn likely assists in individual recognition. Recognizing these grouping structures involves the higher-order process of relating the periods between syllables independent of the syllables' content; by definition, the pauses between within-group syllables are shorter than those between groups. This aspect of song perception underscores the importance of the temporal aspect in sound, especially when analyzing global patterns.

Various advantages can be found in analyzing the similarity of repeating units over time; as already shown, some relations must be done in order to recognize that. As a matter of fact, a great deal of evidence exists to believe that even within a repetitive song, birds perform comparisons of similarity across calls for various advantageous reasons. Botero et al. (2009) cross-correlated repeating units in the spectrogram of the tropical mockingbird (*Mimus gilvus*) to assess the fidelity with which mockingbirds could consistently generate the same sound, finding that alpha males had higher within-type consistency of their song than beta males. In banded wrens (*Thryothorus pleurostictus*), a similar spectrographic analysis was performed that compared the similarity of consecutive within-song trills, augmented by analyzing how individual wrens responded to varying degrees of similarity. Not only was note consistency found to increase over a wren's lifespan, but trills made more artificially similar to each other were successfully discriminated from the originals (de Kort, Eldermire, Valderrama, Botero, & Vehrencamp, 2009).

Another higher-order characteristic of sound animals may analyze lies in the relational arrangement of its simple components. The ability to form and compare sound categories based on order-dependent data within the units has been documented in multiple. A bottlenose dolphin (*Tursiops truncatus*) has been shown to successfully distinguish between sets of auditory stimuli that were either constant or descending in pitch, even with overlapping frequencies between the two sets of sounds (Ralston & Herman, 1995). Humans, in which relative pitch processing and other higher-order functions are widespread as adults (Saffran & Griepentrog, 2001), have shown the ability to identify global patterns and group sounds at as early as 12 months old (Morrongiello, 1986). These results hint that a process exists by which animals can detect the general contour of a sound's dominant frequency, compare relations between individual units or utilize even higher levels of auditory processing.

The ability of birds to perform this same type of task has been called into question. It has been posited that they attend primarily to absolute sound characteristics, such as distinct frequencies in a sound, rather than relational characteristics that require organizing the primary information received from a sound. For example, attempts to teach European starlings (*Sturnus vulgaris*) to learn to discriminate between ascending and descending sequences of frequencies initially failed. One a pitch left the original training range and took a great deal of retraining to teach the birds to learn the discrimination among the novel-frequency stimuli (Hulse & Cynx, 1985). Bregman, Patel, & Gentner (2010), however, showed that by using conspecific song instead of pure tones as the stimuli, pitch shifts outside of the original range were generalized to, implying that songbirds may have specific mechanisms for processing conspecific song as a complex sound; in fact, specialized neurons in starlings were found to respond only to complex

sounds and not pure tones (Müller & Leppelsack, 1985), further supporting that complex sounds can be discriminated differently.

Production of complex calls in columbids is limited but may be of special importance, especially in courtship behavior. A study in ring-necked doves (*Streptopilius risoria*), a Columbidae and vocal non-learner, showed that vocalizations may still play a role in nest-building and mating; perception of the doves' own vocalizations in females may contribute to endocrine stimulation (Cheng, 1991). The vocalizations of pigeons (*Columba livia*) form a limited repertoire. Only two exist for display purposes: a drawn-out nodding call used during nest-building and a quiet tail-drag call used during courtship (Stokes & Lansdowne, 1979). However, perception of vocalizations in pigeons have been implied to be especially important in mating. An audio channel of a male courtship display alone elicited a stronger response in female subjects than a lone video channel (Parton, Yelda, Price, & Shimizu, 2004), hinting strongly that a mechanism for auditory perception and discrimination of complex calls by females would be evolutionary advantageous.

An auditory discrimination task that generated useful discrimination data related to complex sounds was conducted by Cook and Brooks (2009), who successfully trained pigeons (*Columba livia*) in a go/no-go auditory discrimination task that tested pigeons' ability to discriminate between same and different continued presentations of sounds. The birds were presented via in-cage speakers with either a sequence of twelve randomly chosen, equal-duration sounds that differed from each other or corresponding sequences of one random sound repeated twelve times. Different trials, known as S+ presentations, reinforced pecking at a touch screen with grain and same trials, known as S- presentations, did not reinforce pigeons for any behavior.

This paradigm motivated the pigeons to peck only during perceived different sequences and generated a consistent pattern of behavior over the course of a trial, as shown in Figure 3. Pecking begins at a high rate regardless of the trial and continued this way for the first two sounds. However, by the third sound, the rate during S- (same) trials falls drastically while remaining high during S+ (different) trials. By the second half of a trial, the disparity in pecks between same and different trials makes it evident that the birds had successfully learned to discriminate between the two.

While the initial sounds pigeons heard consisted of single notes in a variety of complex timbres, a subsequent transfer test to a set of complex sounds revealed that pigeons were able to carry the discrimination to the new stimuli. This discrimination represented a new step in the testing, as complex timbres consisted of relatively discrete frequencies that could be discriminated on absolute criteria (Figure 3) but, as demonstrated in Figure 2, complex sounds represent constantly changing frequencies that must be integrated into units to be told apart.

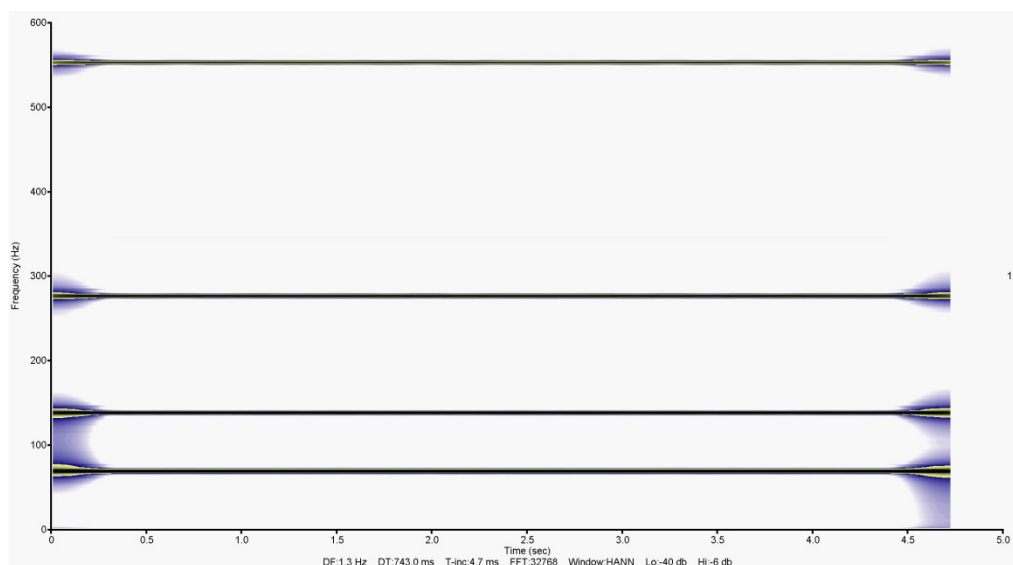
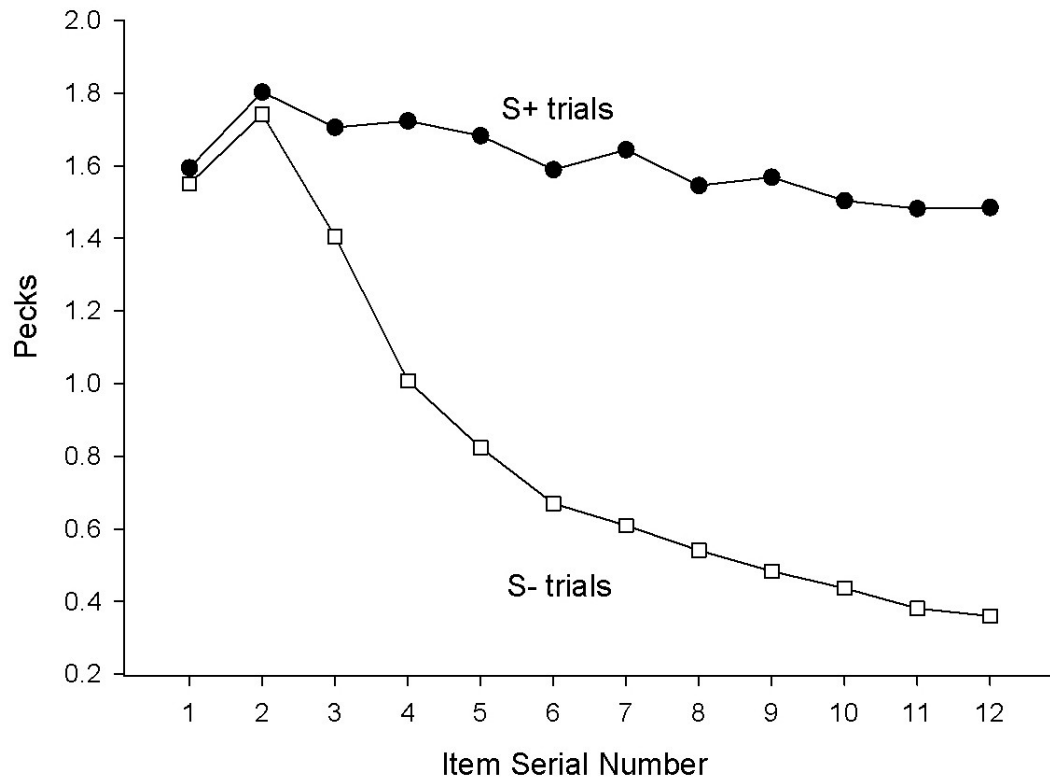


Fig. 3. The spectrogram of a C#4 note (dominant frequency = 278 Hz) in a synthetic Hammond timbre as generated by SONAR, a sound synthesis/editing program. As compared to complex sounds (Fig. 2), frequency bands are more discrete and ostensibly could be discerned on an absolute basis.

Such support that pigeons are capable of discriminating among complex sounds has implications for the motor theory of song perception. Motor theory, as posited for songbirds, states that birds specifically perceive song vocalizations in the light of their own vocalizations, separating them from other types of complex sounds (Williams & Nottebohm, 1985). Showing that non-singing birds can discriminate between heterospecific songs presents an intriguing corollary to motor theory: that vocal production is not an all-inclusive explanation for the ability to perceive complex, if not conspecific, birdsong by avian species.

However, support that pigeons are truly able to perceive and discriminate among complex sounds on a higher-order perceptual basis first requires ruling out that simple lower-order acoustic factors are controlling behavior. By analyzing auditory tests that have occurred since Cook and Brooks (2009) and retroactively obtaining measures of lower-order and complexity-related properties of the sounds originally used, we hoped to discern the factors underlying the pigeons' ability to suppress pecking to a non-reinforced sound presentation.

Examining only same trials, acoustic factors for the the one sound birds were presented with over the trial could be compared to their following suppression response. We hypothesized that the birds were indeed capable of integrating complex sound data and that pecking behavior was not simply elicited as an automatic response to absolute statistics. To test this and truly rule out lower-order effects, a variety of simple and complex acoustic factors were analyzed via multiple linear regression. Were pigeons' responses found to not be controlled by any of the easily quantifiable variables analyzed, it could be reasonably argued that columbids as well attend to global patterns within complex sounds when perceiving similarity.



Method

Animals

Four male pigeons (*Columba livia*) were tested. Two of the birds had served in the experiments described by Cook & Brooks (2009) and two had served in the experiments described by Murphy and Cook (2008). At the start of the experiment, each was highly experienced at performing the auditory same/different task used here. Three pigeons were maintained at 80-85% of free-feeding weight; a fourth pigeon was kept at 85-90% free-feeding

weight due to metabolic concerns. All birds were housed in a standard 12:12 LD environment for the duration of the experiment.

Apparatus

A flat-black black Plexiglas chamber (42.5 cm wide x 44 cm deep x 39.5 cm high) with two speakers (HK-195, Harmon-Kardon) toward the front of each side to play auditory stimuli was used for testing. Speakers played through a 90x120 cm grid of 5 cm holes that formed a plastic grill, and events were controlled using a computer with a sound card (SoundMax Integrated audio card; Analog Devices). Visual stimuli were presented on a color monitor visible beyond a transparent infrared touch screen (EloTouch) in an opening of the front panel. A houselight illuminated the testing area, except during timeouts. A reward of mixed grain was dispensed when appropriate by a food hopper placed in the center of the front panel below the window.

Stimuli

A subset of 70 complex stimuli were analyzed in this experiment. These were drawn from the total pool of auditory stimuli originally used by Cook and Brooks (2009) and a number of subsequently added sounds to their repertoire. These complex sounds came from various CD-ROM or Internet collections of field recordings of birdsong and other sounds. For purposes of categorization within complex sounds, 35 sounds were designated as artificial sounds, 27 sounds as birdsong, and 8 as natural (non-bird) sounds. Sounds varied in sample rate between 8 and 44 kHz and could be either 8 or 16 bits and mono or stereo. Additionally, while all sounds were

truncated to 1.5 seconds of play duration, the amount of silence within this duration varied between sounds and was considered when looking at factors that influenced behavior.

Go-No Go Training

Pigeons were trained using a standard go/no-go procedure similar to that described in Cook and Brooks (2009). Discrimination was between S- trials, *same* sequences of a randomly selected sound repeated 12 times, and S+ trials, *different* sequences of 12 completely different sounds in a random order, as previously described. Sounds were presented for 1.5 seconds each with 50-ms inter-stimulus intervals, the time period between sound presentations. Reinforcement was only provided to S+ trials, while unreinforced probe trials for novel transfers were occasionally interspersed.

Data Selection

To test the factors behind the birds' ability to discriminate complex sounds, data collected from between March 2007 and November 2010 were examined. Once test sessions, partial sessions, and other experiments were eliminated, 450 sessions for each bird were used in our statistical analysis. Within selected sessions, only trials playing all-complex sounds in the S- condition were examined. When looking at trials containing just one sound, any significant predictors could be definitively traced to the effects of the sound's properties. By the same token, different trials did not present a target for analysis as acoustic effects could have resulted from any one of the twelve different sounds presented, constraining analysis to same trials.

Dependent Measures

Several dependent measures were examined as a means of detecting pigeons' responses to stimuli, all reliant on pecking behavior. Total pecks, pecks on the first, second, third, and last items, the amount of time until pecking began, and the pecks during the last five seconds of sound presentation were considered as means of interpreting pigeons' sameness ratings.

Ultimately, pecks over the last five seconds were chosen as the preferred measure. Its late position over the course of the trial ensured that the same-different discrimination had been picked up by the birds, and the data covered a wide enough time that it did not fail to correlate highly with the total number of pecks, $r(68) = .967, p < 0.05$.

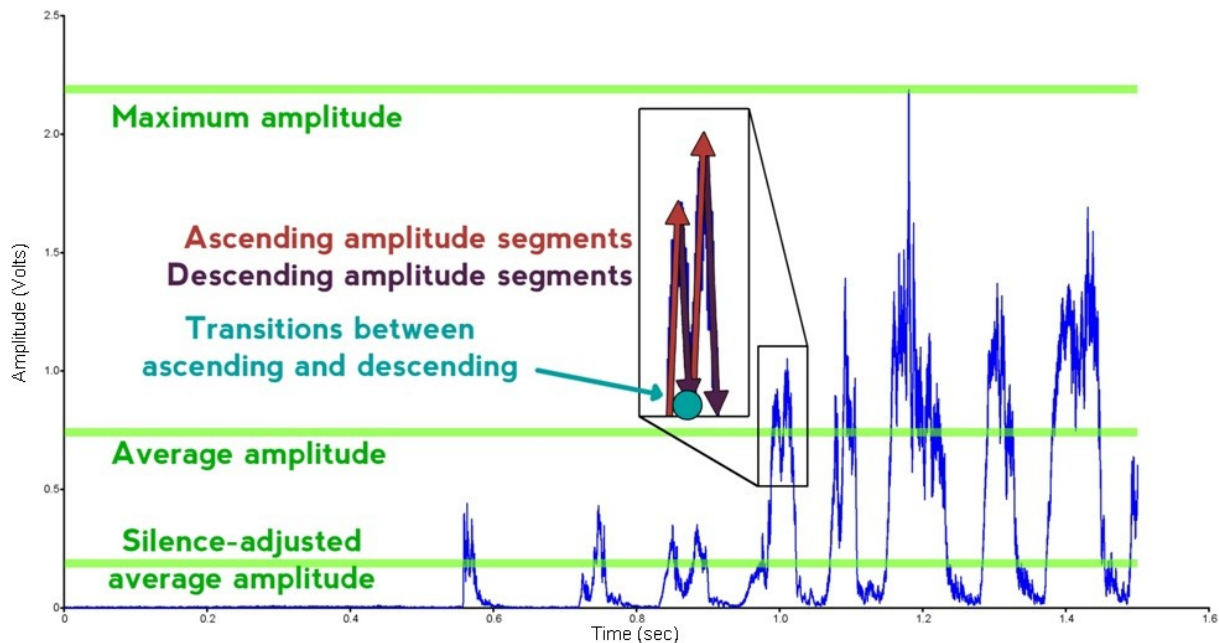
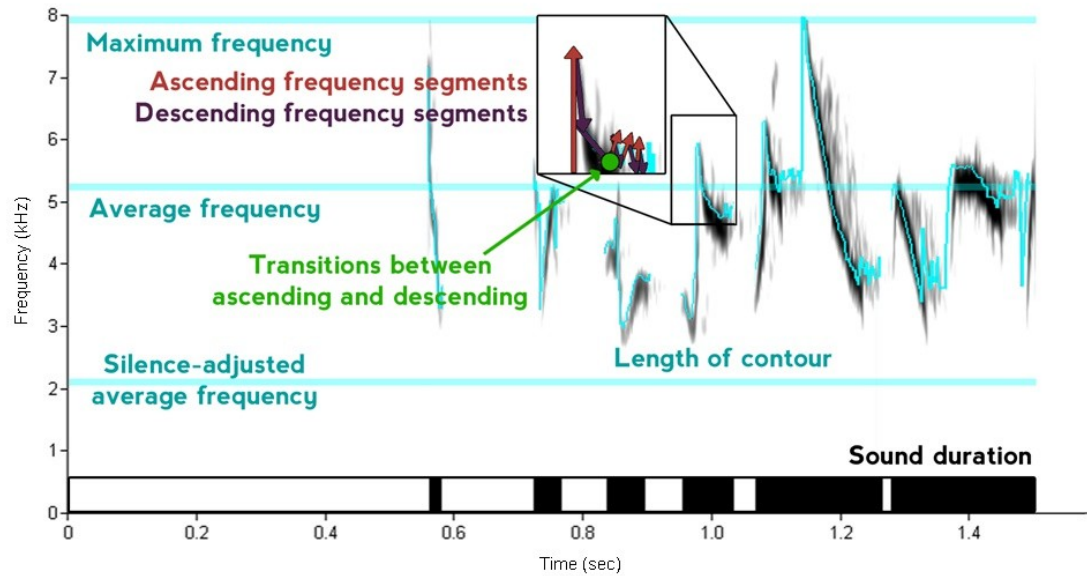


Fig. 5. A visual representation of the amplitude envelope (blue line) as created by SIGNAL, as well as examples of several types of variables relating to the amplitude of the sound. Amplitude in Volts is plotted against time in seconds.



Acoustic Analysis

Information about sound pitch and amplitude was analyzed using a bioacoustical analysis program (SIGNAL 5, Engineering Design, Berkeley, CA). Several analyses were done directly from the spectrogram, allowing for a wide variety of basic information to be calculated about each sound. Figures 5 and 6 present a visual representation of all the possible variable permutations considered and calculated; from these, nine considered to be representative of the sound were chosen for analysis; their results for each of the 70 sounds are listed in Appendix A.

Several analyses were readily conducted directly from the spectrogram before further transformations were performed.

- **Sound duration** was measured as the total number of time the amplitude exceeded 2% of its maximum value. Not to be confused with the total playtime of 1.5 seconds each sound was truncated to, this value indicated the amount of time a sound was actively playing above this amplitude threshold.

- **Autocorrelation** consisted of a cross-correlation run on the same sound; that is to say, one copy of the sound kept at a constant point in time was compared with a second copy at variable time offsets. This produced a function that gave the correlation of a sound with itself as a function of time offset for one of the copies. By measuring the area under the curve at each sound sampling interval, a value attempting to quantify self-similarity on a simple measure was calculated.
- **Silence-adjusted frequency** was calculated using SIGNAL's default method of average frequency, using all values in the 1.5-second allotment for the sound as considered frequencies. The default method counted the sound's functionally silent intervals being as a period of zero frequency, depressing the value as a function of silence present.
- **Average frequency** was a result of dividing the silence-adjusted frequency by the percentage of the 1.5-second interval the sound was actively playing, determined by the sound duration calculation. This value was meant to approximate the average frequency of the active sound disregarding interspersed silence.

For more complicated frequency analysis, the dominant frequency contour of the sound, known as the spectral contour, was calculated with SIGNAL's Spectrogram Contour Detection. The spectral contour function was established by using only frequencies above an amplitude cutoff at 40 dB below the signal maximum and continuing over the time course of the sound to find adjacent dominant frequencies. This gave a final shape that roughly traced the main pitch over the sound's progression.

- **Bandwidth** came from the difference between the maximum and minimum frequency values that the spectral contour covered. The final value represented the frequency range in Hertz above the aforementioned amplitude threshold.
- **Net ascending frequency segments** represent an additive value equal to the number of samples in which the spectral contour indicated that frequency was increasing minus the number of samples in which the frequency was decreasing, with the result divided by the overall sampling rate. The final value represents roughly the amount of time in seconds spent ascending, with negative values indicating a net descent in frequency.
- **Frequency transitions** represent the number of times frequency changed from ascending over the course of one sample to descending. While it looked at similar data to net ascending frequency segments, it measured continuous change in frequency and attempted to quantify the rate of modulation.

A function called an amplitude envelope (Figure 5) was derived from the initial amplitude-time function and used for purposes of amplitude analysis. To obtain the amplitude envelope, the intensity of the original waveform, in which amplitude oscillates between positive and negative peaks, was converted to all-positive values. The envelope followed the rise of the original waveform equation identically but never dropped slower than a predetermined exponential rate based off the signal bandwidth. This predetermined decreasing rate allowed the envelope to ignore minute sinusoidal variations and have a continuous form over insignificant gaps.

- **Silence-adjusted amplitude** corresponds in its method of measurement to its frequency counterpart, where non-active regions of the sound depressed the average value.
- **Average amplitude** corrected for the effects of interspersed silence by dividing by the portion of time the sound spent actively playing, the same method used to calculate average frequency.

Results

Several findings came about as a result of the analyses of pigeons' ability to suppress pecking responses to nonreinforced same trials. First, it was established that pigeons had continued to successfully discriminate between complex sounds, ruling out that any observed effects were due to an overall, non-differential suppression of response. Second, while the birds discriminated between same and different trials for all sounds, they suppressed better to some sounds than others, agreeing in their responses, and the birdsong sound category was found to suppress better than artificial sounds. Finally, a linear regression was run to test the effectiveness of nine acoustic properties (Appendix A) as predictors for pecks over the last 5 seconds on same trials but failed to explain the majority of variance in the data.

Discrimination

Before any subsequent analysis can be done, the fundamental assumption that pigeons discriminated between same and different trials had to be addressed to make certain that any type of comparison was being made in the first place. The birds successfully discriminated between same and different trials for the complex sounds presented to them as evidenced by a wide

difference in their mean pecks over the last 5 seconds between different ($M = 4.17$) and same ($M = 1.19$) trials. A paired t-test discovered that the differential responses in pecking across different types of trials was significant ($t(69) = 38.873, p < 0.05$).

Another assumption behind the interpretation for all following results is that the observed peck suppression is a result of sound repetition and not a first-item bias. A lack of significant correlation ($r(68) = -.121, p = .317$) between pecks over the last five seconds and pecks on the first sound for each sound ensured that an initial item bias was not responsible for any variations observed.

Prediction by Acoustic Factors

Ordering by pecks over the last five seconds on same trials of each sound's consecutive presentations created an order indicative of how well birds suppressed pecking to repetitions of each sound across a sequence. When a series of bivariate correlations was run between all four birds tested, responses correlated significantly in the order by which they were able to suppress

	B ₁	L ₂	N ₃	N ₄
B ₁	---	---	---	---
L ₂	.610	---	---	---
N ₃	.389	.588	---	---
N ₄	.460	.468	.556	---

Table 1. A half-matrix of bivariate correlations of the four birds tested based on their responses' sound ranking. All correlations were significant ($p < 0.05$).

to the different sounds (Table 1), suggesting that properties inherent in the sounds and how the birds processed them rather than individual preferences account for the differential suppression.

Next, to test if the inherent sound properties being attended to were part of a discrete set of quantifiable local variables, the nine acoustic factors described in the methods section were

analyzed to determine their effect on the pecks pigeons made during the last five seconds of each same trial. To obtain this information, a multiple linear regression assessed each variable's strength as a predictor of pecking behavior both individually and as a whole. The regression provided an advantage over a simple correlation matrix in that it accurately eliminated any variance redundantly accounted for by multiple variables and presented a realistic depiction as to how well the nine properties quantified explained variable pecking behavior over the different sounds.

The first method used, known as stepwise entry, assessed each sound variable individually to determine which had the highest bivariate correlation with end-trial pecks and entered them into a regression model, repeating this procedure until the additional variance explained with each entry was no longer significant at the level of $p < 0.05$. Only silence-adjusted frequency demonstrated any significance as a predictor, though it explained less than one-fifth of the observed variance ($R^2 = .198$, $F(1,68) = 16.813$, $p < 0.05$). Its strength as a predictor was indicated by its beta value in the regression model ($b = -.445$), which indicated how many standard deviations the pecks increased for every standard deviation the silence-adjusted frequency increased; the negative value indicates an inverse correlation, though a statistically significant one ($t(68) = -4.1$, $p < 0.05$). Overall, despite the statistical significance of the model's predictive power and range, just over 80% of the differential pecking remained unexplained by any significant predictors.

To test for absolute certainty that no combination of lower-order variables could account for a majority of the data, all nine variables were used in a regression model regardless of how small their added variance was. Using this more liberal method of accounting for variance, just over a quarter of pecking behavior was accounted for ($R^2 = .278$) in a significant model ($F =$

2.571, $p < 0.05$); the obtained beta values for each variable may be found in Appendix B.

Despite adding every segment of incremental variance, insignificant or not, the second method of regression again failed to account for a vast majority of the difference in pecking, favoring an explanation that the behavior observed in response to repetitive sound presentation could not be explained by any one component of sound, but perhaps instead to a higher-order, integrative characteristic not quantified.

Category Effects

One question was if the difference in responses translated to the category of the sound as well. A between-groups ANOVA found significant difference in end-trial pecking across the categories of birdsong ($M = .904$), artificial ($M = 1.18$), and natural ($M = 1.26$) sounds, ($F(2, 67) = 5.752, p < 0.05$). To isolate the difference, a one-way ANOVA was performed with natural

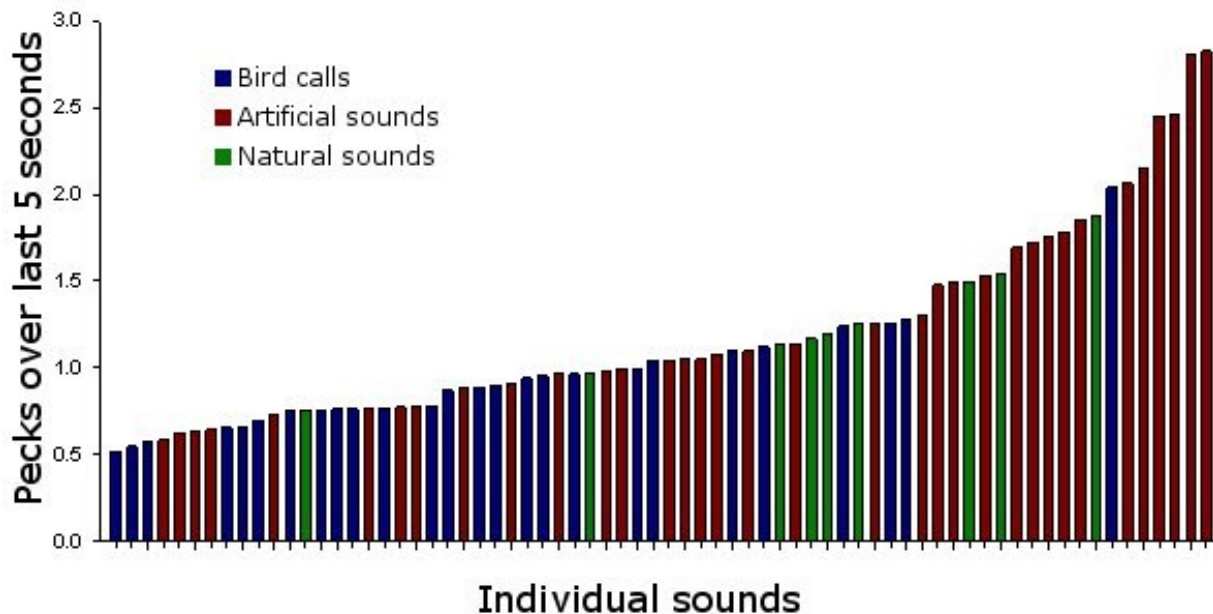


Fig. 7. The ability of birds to suppress responses on nonreinforced trials based off of the sound category. A significant difference was found between responses to bird calls versus artificial sounds.

	Bird calls	Artificial sounds	Natural sounds
Silence-adjusted frequency (Hz)	1644	1295	1045
Average frequency (Hz)	3609	1697	1158
Silence-adjusted amplitude (V)	0.193	0.268	0.159
Average amplitude (V)	0.445	0.345	0.206
Sound duration (ms)	777.369	1217	1285
Net ascending frequency segments	-0.004	-0.013	0.007
Bandwidth (Hz)	3914	3722	3297
Frequency transitions	0.288	0.423	0.219
Autocorrelation	0.228	0.623	0.522

Table 2. Averages of each category along the nine acoustic measurements analyzed. Units are listed where appropriate. Bird calls score significantly higher than artificial sounds in silence-adjusted frequency, the variable found significant in the stepwise multiple linear regression.

sounds removed, and bird calls and artificial sounds were found to differ significantly in the number of pecks accrued, ($F(1, 68) = 10.419, p < 0.05$). From visualizing the response ranking as a result of category (Figure 7), it becomes readily apparent that bird calls were more readily suppressed to during repetitive play than were artificial sounds.

To explain the effect found for silence-adjusted frequency, its values were compared between bird calls and artificial sounds. Bird calls ($M = 1644$ Hz) had a higher average value of silence-adjusted frequency ($M = 1644$ Hz) than did artificial sounds ($M = 1295$ Hz), though they stopped short of doing so on a significant basis ($F(1,69) = 3.168, p = 0.08$). The correlation matches with the fact that birds both suppressed better on bird calls and on higher frequencies, though it does not establish causality in either direction.

Discussion

The pigeons successfully picked up the discrimination between complex sounds, a significant finding given that sound integration is a temporal task, yet complex sounds continuously change over the course of time. Interestingly, the birds' ability to suppress responses on same trials was differential across the sounds. This variability in response rate correlated extremely well among the birds and was shown to be a response of repetition rather than a bias on the first sound; these data suggests that the differences in pecks are due to an overreaching mechanism rather than individual differences. When pecks over the last five seconds were regressed over several possible sound features, only 27.8% of the variance in the data was explained, and only silence-weighted frequency contributed a statistically significant amount to the R^2 value; in all forms of the regression, a majority of the data was left unexplained by lower-order variables. The ranking pattern was found to be influenced towards specific categories of the sounds; namely, birdsong generally suppressed same responding better than did artificial sounds and was loosely tied to higher silence-adjusted frequencies.

The ability of columbids to successfully discriminate between same and different sequences of complex sounds, including birdsong, has important implications for the motor theory of song recognition in oscine birds. Originally proposed to account for parallel processing in human speech, this motor theory posits that the brain areas involved in song production at the neuromotor level also play a role in its perception and recognition, predicting that birds are especially adapted to hear their own song and have the best discrimination among conspecific vocalizations due to vocal motor involvement (Lieberman, Cooper, Shankweiler, & Studdert-Kennedy, 1967). Subsequent experiments in songbirds have hinted at an interaction between auditory and motor regions. The HVC, an area of the brain in songbirds closely associated with song production, has been shown in white-crowned sparrows to be responsible

for not only song production but recognition of self, conspecific, and interspecific birdsong (McCasland & Konishi, 1981). Williams and Nottebohm (1985) discovered that the tracheosyringeal part of the hypoglossal motor nucleus, used by zebra finches to sing, was also active when listening to pure tones. This finding, in addition to supporting evidence of the HVC's activity, led them to expand motor theory to suggest that birds, too, discriminate between conspecific sounds by referring to their vocal generation centers. The HVC, along with related connections, has been strongly tied to vocal learning as an auditory feedback circuit (McCasland & Konishi, 1981; Grace, Amin, Singh, & Theunissen, 2003). However, a connection between auditory input and the areas of the brain responsible for vocal control has yet to be discovered in pigeons (Wild, 1994) and the HVC is generally regarded as less complex if not missing in non-oscine birds (Farries, 2001).

Questions as to motor theory's ability to fully explain song discrimination have already been raised in female canaries. Though their HVC was shown to be active during song discrimination tasks, they have not developed the same motor connections for vocalizations that males have, suggesting motor activation is not a necessity for complex sound recognition (Brenowitz, 1990); the current study supports these results and adds to a growing pool of avian species that can successfully pick up a discrimination among complex sounds that they are unable to produce. Furthermore, budgerigars, psittacines that learn vocalizations but do not sing, have a vocal control circuit independent from those of songbirds (Striedter, 2004) yet successfully perform discrimination tasks involving pure tones and complex vocal signals (Dooling, Park, Brown, & Okanoya, 1987; Brown, Dooling, & O'Grady, 1988). The discrimination between different songs and the recognition of repetitions of the same bird songs by pigeons, birds without the traditional neuronal structure for song recognition and vocal non-

learners (Wild, 1997), strongly reinforces the possibility that the activation in the HVC and other vocal areas of the brain previously associated with song recognition is not the exclusive action by which birdsong may be recognized. Possible studies using neural recording methods such as microelectrodes in pigeons could give more information as to how birds without an auditory-vocal feedback circuits manage to accomplish discrimination between songs without having the motor skills to generate them. Additionally, pigeon vocalizations could be interspersed with the sounds to see if pigeons generate a different response to conspecific calls, which were initially omitted to avoid complications relating to conspecific recognition.

The final regression's finding that silence-adjusted frequency is was the best predictor than any other acoustic feature was expected based on the results of the past experiments showing the importance of lower-order sound comparisons in some settings. Frequency also plays a role in categorization and has been found multiple times to be the most important criterion by which birds attempt to differentiate sounds. The field sparrow (*Spizella pusilla*), when tasked with discriminating between sounds that differ along one of five features, are most sensitive to changes in song frequency (Nelson, 1988). Auditory discrimination tasks with Great Tits (*Parus major*) revealed that they will preferentially use frequency as the measure by which they determined similarity of novel, modified songs to one of two training songs in an operant procedure unless the amount by which the modified calls differed in another property exceeded that of frequency. When calls were experimentally made to randomly differ evenly among one random manipulated feature, frequency and amplitude modulation were more significantly used than other variables (Weary, 1991).

Alternately, the correlation between higher frequency and suppressive response to repetition could be an effect of the frequency falling into the auditory threshold at which pigeons

are best able to perceive sound, thought to fall within 200-4000 Hz (Wit, Scheurink, & Bleeker, 1985). Finally, it may be that an intrinsic organizational factor in birdsong allowed for better suppression on same trials by the birds and aided in discrimination. As mentioned, birdsong represents a highly-ordered form of complex sound and may prove to be a more easily suppressible target to pigeons independent of absolute value of frequency but rather due to its distinct organization independent of these lower-order factors. According to Appendix B, birdsong has a higher frequency than the other types of sounds used, however, and better suppression to birdsong would have caused the observed correlation between frequency and pecks. This data is in agreement with previous findings that environmental and artificial sounds tend to be lower in frequency than natural calls such as birdsong (Lewinski, 2002).

Two possible experimental setups could help separate out the cause of this effect. Pitch-shifting birdsong and artificial sounds that performed at extremes and assessing if response rates adjust strongly to the change in lower-order characteristics would test for an effect of absolute frequency. Should a frequency-related variable truly control the pigeons' repression response, one would expect to see decreasing pecks on same trials as the frequency of the repeated sound was artificially raised. However, should a global pattern recognition system be at play like was hypothesized at the beginning, the organizational structure that the pigeons draw from to integrate the repeating sound into units

The fact that the frequency variable that took silence into account was a better predictor for ability to suppress pecks also hints that a weighted combination of duration and frequency is being attended to. The mixing of acoustic features with how much silence is present within the sound has not been significantly addressed in recent literature, though evidence exists to believe that birds may be paying attention to it. The presence of silence in seemingly continuous

birdsong has been documented in early field studies as varying from less than half the time spent singing to comprising over 80% of the song's duration depending on the species of bird (Hatshorne, 1956). This natural difference between calls combined with correlations between the body size of different species and their frequency constraints (Wallschlager, 1980) could mean that birds pay attention to a combined version of the information present in each to discriminate between different calls.

Another form of silence present in the experiment, the inter-trial interval of 50 milliseconds between sounds, presents an interesting factor that has not been taken into account due to its constancy across the experiment. Manipulations on this interval to tax memory and observe its effects on discrimination could potentially bear fruitful results; memory's involvement in relational auditory discrimination has support in a study that found infants initially able to discriminate between sounds based on relational properties lost the ability when given a task designed to place greater cognitive stress on memory (Trehub, 1984). While pigeons are able to retain information across gaps in sound by the 50 ms used in this experiment and longer (unpublished data), increasing the ITI would test for how strongly memory figures in the task and produce valuable psychoacoustic data for the timeframe of auditory comparisons.

Another limitation to be corrected in future studies lies in the unequal weighting of the sound categories. While bird calls ($N = 27$) and artificial sounds ($N = 36$) were well-represented in the sample of stimuli, natural sounds were relatively scarce ($N = 9$). However, starlings have been shown to have a specialized neural response to conspecific calls (Cousillas, Leppelsack, Leppelsack, Richard, Mathelier, & Hausberger, 2005) separate from general complex sound processing, and literature in complex sound processing sorely lacks experiments in which subjects discriminate between different heterospecifics, especially nonbird natural sounds. As

animal calls, sounds categorized as natural are more likely to have harmonic intervals rather than the broadband non-harmonicity of artificial/environmental sounds (Lewicki, 2002). They are also typically shorter; however, all sounds were arbitrarily truncated at 1.5 seconds for this study. This inter-category difference also brings up the possibility that further discrimination criteria may be discovered with sounds permitted to last longer.

Without information on presentations of different sounds, however, it is only possible to claim that observed factors do or do not play a role in a sound's suppression following repetition and cannot say anything about discrimination, which involves both same and different trials. The current setup, which uses twelve different sounds in a pattern like ABC...JKL, makes it extremely difficult to analyze for the effects of any one sound on a response as observed effects would be the result of a mix of all twelve sounds' influence on the pigeons' perceptual system. To overcome this variable, further studies could employ a presentation scheme known as ABAB that alternates all possible permutations of sound pairs with only two different types of sounds played per S+ (different) trial. In this experimental setting, both similarity and difference scores for each sound could be analyzed and compared back to the simple acoustic features analyzed in this study.

More important, perhaps, than any of the obvious findings is that the selected lower-order and relational variables fail to account for an overwhelming majority of the data (72.2%). All the same, the sound ranking correlated significantly among all four birds tested, eliminating any effects of individual idiosyncrasies and implying that the differential responses arose as a result of the properties inherent in pigeons' auditory processing. The responses given to the sounds seem to take into account not any one property of sounds but a global property that consists of more than simply the sum of a sound's parts. Despite frequency's categorical importance,

budgerigars have been found to discriminate between conspecific calls that lie within the same narrow frequency range (Dooling et al., 1987). Furthermore, in a similar vein to this study, the budgerigars were able to discriminate between different calls within a heterospecific (Park & Dooling, 1985). Looking beyond birdsong, pigeons have been shown to discriminate between different musical structures in the form of compositions by Bach and Stravinsky, generalizing the discrimination independent of factors like timbre (Porter & Allen, 1984).

Further evidence could be gathered to support that pigeons can attend to global patterns in complex sounds independent of absolute properties by generating a set of experimentally manipulated stimuli that disrupted higher-order features, such as reversing and scrambling sound components. Looking back at the concept of the spectrogram, one can imagine that while the total and average values of frequency and amplitude present in the columns would remain unchanged as nothing was added or removed, the temporal and potentially organizational properties of the sound would be critically changed. If the birds were attending to absolute values independent of how they relate to each other over the course of the sound, it could be expected that the new sounds would elicit no different a response than their scrambled counterparts. However, a different response in reaction to these sounds would indicate that the overall structure of the sound is indeed being attended to by the pigeons. The latter is a distinct possibility and has some limited support in other animals; lemurs that usually employ an anti-predator response to a hawk call failed to do so when the call was reversed (Macedonia & Yount, 1991). In pigeons, then, poor suppression of a song's scrambled or reversed version compared to the original would support similar higher-order perception of sounds.

Pilot data from an ongoing study (unpublished data) further supports the idea that pigeons' cognitive systems are capable of supporting the integration of sounds over time.

Sequences of hammond notes were played in four different orders: up twelve half steps (according to the diatonic scale), down twelve half-steps, up six half-steps followed by down six half-steps, or down six half-steps followed by up six half-steps. The stimuli were played at varying tempos for the same total time and inserted as probe trials into the pigeons' auditory experiments.

As the tempo increased, pigeons pecked less on these trials, insinuating that they were increasingly viewing the note sequences as grouped units instead of individual notes. The latter two sequences of up six, down six and vice versa presented a much more pronounced effect, despite the fact that all four types of stimuli consisted of constantly changing notes. However, due to the return to the original note of the up-down/down-up sequences, the latter two were more continuous. The suggestion that pigeons may be attending to this property calls for further investigation into their ability to group sounds, possibly representative of a higher cognitive capacity in the auditory domain than has been investigated previously.

Combined with the findings from the current study, this growing body of evidence supports a mechanism for perceiving complex sounds as whole sounds, integrative units independent of auditory features and arising from processes distinct from those adapted for conspecific recognition. It would be extremely unlikely that this mechanism has not evolved, given the wealth of information present in complex sounds in every sound from birdsong to human music. It remains for future research to delve further into the field of complex audition and discover how widely among animals this whole-sound integration ability exists and elucidate further just how intricate such a process could be.

Appendices

Sound name	Category	Silence-adjusted frequency (Hz)	Average frequency (Hz)	Silence-adjusted amplitude (Volts)	Average amplitude (Volts)	Sound duration (ms)	Net ascending frequency segments	Frequency transitions	Bandwidth (Hz)	Autocorrelation
Alder flycatcher	Bird call	710.9405	3985.822329	0.096810289	0.54275796	267.551	0.031	0.124	3872.54808	0.098761
American pipit	Bird call	568.2481	6130.074521	0.074359822	0.80216942	139.0476	-0.086	0.008	4153.92773	0.020903
Bang	Artificial	125.6841	200.3998406	0.074895025	0.11941806	940.75	-0.013	0.093	355.20057	0.401795
Bark	Natural	78.5275	283.4239531	0.102051714	0.3683283	415.6009	0.003	0.065	1078.15937	0.107843
Bell ting-ting	Artificial	1762.9785	2928.851952	0.465077443	0.77263732	902.9025	0.017	0.625	7382.09653	0.699167
Bird	Bird call	1221.3099	1912.814947	0.113515876	0.17778851	957.7324	0.07	0.12	1628.02698	0.197259
Black rail	Bird call	518.7663	1998.391963	0.097478675	0.37550743	389.3878	-0.023	0.146	1329.63928	0.109882
Blast	Artificial	174.6846	175.0126671	0.076513577	0.07665727	1497.1882	0.004	0.379	685.803249	1.060451
Bluegray gnatcatcher	Bird call	1333.1009	6830.721436	0.234938622	1.20381007	292.7438	-0.041	0.103	3326.72168	0.15414
Bluewinged warbler	Bird call	4389.6472	7027.47285	0.331455713	0.53063399	936.9614	0.111	0.415	6195.29761	0.463604
Canada warbler	Bird call	2144.7325	4999.085912	0.196372031	0.45771706	643.5374	-0.078	0.159	5134.21973	0.089715
Cappuccino machine	Artificial	3452.5477	3955.489812	0.258232683	0.29585015	1309.2744	0.057	0.478	10895.6151	0.348989
Car horn	Artificial	2298.572	2335.645862	0.843865605	0.85747639	1476.1904	-0.018	0.628	2643.17411	1.14525
Car start	Artificial	942.9944	966.8626287	0.265226283	0.27193945	1462.9706	0.046	0.559	6449.29037	0.300362
Cardinal	Bird call	2196.9808	2606.587419	0.303762499	0.36039619	1264.2857	0.084	0.339	3998.21049	0.229261
Cat	Natural	732.8935	1455.009261	0.147202449	0.29224018	755.5555	-0.16	0.075	1725.98541	0.302804
Cell phone	Artificial	1815.1579	3701.263595	0.276883628	0.56458961	735.6236	-0.007	0.548	7099.54613	0.337062
Chachalaca	Bird call	964.2476	1530.680356	0.18904999	0.30010456	944.9206	-0.006	0.524	2852.75538	0.414422
Church bells	Artificial	1241.1761	1270.425704	0.453807596	0.46450204	1465.4648	0	0.606	2803.00549	0.953914
Clapper rail	Bird call	643.703	660.3131328	0.054630308	0.05603999	1462.2676	0.003	0.674	5085.82671	0.163299
Common gallinule	Bird call	1179.2345	1181.86091	0.192744392	0.19317368	1496.6666	-0.024	0.489	2060.46632	0.367031
Common	Bird call	1612.3324	1612.3324	0.382328949	0.38232895	1500	-0.214	0.511	5636.0	0.382842

Palm warbler	Bird call	3168.1197	6248.39365	0.192353086	0.3793726	760.5442	-0.043	0.207	3901.5	0.150812
Party horn	Artificial	929.9945	929.9945	0.197859648	0.19785965	1500	-0.054	0.343	3711 1827.0	0.812107
Phone ringing	Artificial	1110.7557	4113.334133	0.167159842	0.61902386	405.0567	0.018	0.232	6443 7966.5	0.244823
Piedbilled grebe	Bird call	595.1388	1100.722251	0.221032764	0.40880494	811.0204	0.034	0.249	0787 822.16	0.437215
Piglet squeal	Natural	2112.4485	2113.239697	0.183982182	0.18405109	1499.4384	0.098	0.358	9617 6597.9	0.300036
Radio static	Artificial	323.3725	323.3725	0.237150871	0.23715087	1500	-0.078	0.566	3668 1614.6	0.828482
Redtailed hawk	Bird call	1729.5577	2481.461089	0.378532217	0.54309432	1045.4875	-0.017	0.44	6005 3013.6	0.6121
Revving	Artificial	143.6931	143.6974492	0.122275798	0.1222795	1499.9546	-0.01	0.281	469 845.55	0.617793
Sanderling	Bird call	1155.5018	2347.051812	0.140285561	0.28494761	738.4808	0.031	0.276	0846 5314.2	0.044306
Spring	Artificial	420.9857	1057.740967	0.066674788	0.16752269	597.0068	0.019	0.093	0356 1715.6	0.201634
Tea break	Artificial	2551.3911	3801.913043	0.352367268	0.52507423	1006.6213	-0.007	0.416	9092 9676.3	0.361048
Clock ticking	Artificial	339.6651	345.8607809	0.162670148	0.16563734	1473.1293	-0.009	0.603	1293 983.37	0.952759
Toilet flush	Artificial	1122.7201	1133.671136	0.201325835	0.20328957	1485.5103	0.016	0.572	2551 3922.4	0.50109
Typing	Artificial	1460.5939	1628.242648	0.103699865	0.11560266	1345.5555	0.033	0.513	2889 4839.1	0.527735
Vacuum	Artificial	1077.0203	1077.0203	0.269351899	0.2693519	1500	0.009	0.548	408 4550.2	0.83742
Wasp	Natural	348.0068	348.6333872	0.136089757	0.13633479	1497.3041	0.022	0.237	8325 993.95	1.041087
Water boiling	Artificial	1570.0977	1654.88054	0.226406815	0.23863243	1423.152	-0.011	0.526	7685 4202.3	0.575034
Whimbrel	Bird call	1688.8715	2808.41759	0.185506921	0.30847871	902.0408	0.004	0.424	8399 2546.9	0.352937
Whip	Artificial	534.1375	1307.024878	0.088091848	0.21555917	613	0.008	0.109	8743 2661.1	0.151718
Whistle	Artificial	1710.1612	2546.07419	0.12530348	0.18655081	1007.5283	0.025	0.133	9733 2647.8	0.749579
Willet	Bird call	1619.4864	2747.179968	0.25362602	0.4302329	884.263	0.007	0.303	9955 3588.3	0.283663
Wood duck male	Bird call	3155.9359	6086.093162	0.171125878	0.33000925	777.8231	-0.005	0.268	5336 5504.2	0.180857
Wormeating warbler	Bird call	4764.3177	5226.181107	0.157364065	0.17261928	1367.4376	0.05	0.313	4365 4556.7	0.337536
Zip	Artificial	858.9313	1077.451096	0.07519882	0.09433007	1195.7823	0.042	0.272	3975 1593.1	0.586736
									8658	

Appendix A. The values of the nine parameters used on the regression for each of the 70 measured sounds.

Predictor	Beta	T	Significance
Silence-adjusted frequency	-.182	-.483	.631
Average frequency	-.428	-1.049	.298
Silence-adjusted amplitude	-.316	-.759	.451
Average amplitude	.352	.787	.434
Sound duration	-.143	-.537	.594
Net ascending frequency segments	.122	1.066	.291
Frequency transitions	.125	.823	.414
Bandwidth	.169	.991	.325
Autocorrelation	.185	.928	.357

Appendix B. Results of the last 5 seconds of pecks in a trial regressed over nine variables relating to acoustic properties. All variables were inserted as predictors regardless of how significant the variance they added to the model was.

References

- André, M., & Kamminga, C. (2000). Rhythmic dimension in the echolocation click trains of sperm whales: A possible function of identification and communication. *Journal of the Marine Biological Association of the United Kingdom*, 80(01), 163.
- Botero, C. A., Rossman, R. J., Caro, L. M., Stenzler, L. M., Lovette, I. J., de Kort, S. R., et al. (2009). Syllable type consistency is related to age, social status and reproductive success in the tropical mockingbird. *Animal Behaviour*, 77(3), 701-706.
- Bregman, M. R., Patel, A. D., Gentner, T. Q. (2010). Pitch shifting does not disrupt song recognition in the European Starling. Unpublished paper presented at the 11th International Conference on Musical Perception and Cognition, Seattle, WA.
- Brenowitz, E. (1991). Altered perception of species-specific song by female birds after lesions of a forebrain nucleus. *Science*, 251(4991), 303-305.
- Brown, S. D., Dooling, R. J., & O'Grady, K. (1988). Perceptual organization of acoustic stimuli by budgerigars (*Melopsittacus undulatus*): III. contact calls. *Journal of Comparative Psychology*, 102(3), 236-247.
- Cheng, M. F. (1992). For whom does the female dove coo? A case for the role of vocal self-stimulation. *Animal Behaviour*, 43, 1035-1044.
- Cook, R. G., & Brooks, D. I. (2009). Generalized auditory same-different discrimination by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, 35(1), 108-115.
- Dawson, S. M. (1991). Clicks and communication: The behavioural and social contexts of Hector's dolphin vocalizations. *Ethology*, 88, 265-276.
- de Kort, S. R., Eldermire, E. R. B., Valderrama, S., Botero, C. A., & Vehrencamp, S. L. (2009). Trill consistency is an age-related assessment signal in banded wrens. *Proceedings of the Royal Society B: Biological Sciences*, 276(1665), 2315-2321.

- Dooling, R. J., Brown, S. D., Park, T. J., Okanoya, K., & Soli, S. D. (1987). Perceptual organization of acoustic stimuli by budgerigars (*Melopsittacus undulatus*): I. pure tones. *Journal of Comparative Psychology, 101*(2), 139-149.
- Dooling, R. J., Park, T. J., Brown, S. D., Okanoya, K., & Soli, S. D. (1987). Perceptual organization of acoustic stimuli by budgerigars (*Melopsittacus undulatus*): II. vocal signals. *Journal of Comparative Psychology, 101*(4), 367-381.
- Farries, M. A. (2001). The oscine song system considered in the context of the avian brain: Lessons learned from comparative neurobiology. *Brain, Behavior, and Evolution, 58*(2), 80-100.
- Grace, J. A., Amin, N., Singh, N. C., & Theunissen, F. E. (2003). Selectivity for conspecific song in the zebra finch auditory forebrain. *Journal of Neurophysiology, 89*(1), 472-487.
- Hartshorne, C. (1956). The monotony-threshold in singing birds. *The Auk, 73*, 176-192.
- Hulse, S. H., & Cynx, J. (1985). Relative pitch perception is constrained by absolute pitch in songbirds (*Mimus*, *Molothrus*, and *Sturnus*). *Journal of Comparative Psychology, 99*(2), 176-196.
- Lemon, R. E. (1977). Bird song: An acoustic flag. *Bioscience, 27*(6), pp. 402-408.
- Lewicki, M. S. (2002). Efficient coding of natural sounds. *Natural Neuroscience, 5*, 356-363.
- Lieberman, A. M., Cooper, F. S., Shankweiler, D. P., & Studdert-Kennedy, M. (1967). Perception of the speech code. *Psychological Review, 74*(6), 431-461.
- Lilly, J. C., & Miller, A. M. (1961). Sounds emitted by the bottlenose dolphin. *Science, 133*(3465), 1689-1693.
- Macedonia, J. M., & Yount, P. L. (1991). Auditory assessment of avian predator threat in semi-captive ringtailed lemurs (*Lemur catta*). *Primates, 32*(2), 169-182.

- Mager III, J. N., Walcott, C., & Piper, W. H. (2007). Male common loons, *Gavia immer*, communicate body mass and condition through dominant frequencies of territorial yodels. *Animal Behaviour*, *73*(4), 683-690.
- McCasland, J. S., & Konishi, M. (1981). Interaction between auditory and motor activities in an avian song control nucleus. *Proceedings of the National Academy of Sciences of the United States of America*, *78*(12, [Part 2: Biological Sciences]), pp. 7815-7819.
- Mersohn, D. H., & King, L. E. (1975). Intensity and reverberation as factors in the auditory perception of egocentric distance. *Perception and Psychophysics*, *18*(6), 409-415.
- Miyazaki, M., & Waas, J. R. (2003). Acoustic properties of male advertisement and their impact on female responsiveness in little penguins *Eudyptula minor*. *Journal of Avian Biology*, *34*(3), pp. 229-232.
- Morrongiello, B. A. (1986). Infants' perception of multiple-group auditory patterns. *Infant Behavior and Development*, *9*, 307-319.
- Müller, C. M., & Leppelsack, H. J. (1985). Feature extraction and tonotopic organization in the avian auditory forebrain. *Experimental Brain Research*, *59*, 587-599.
- Murphy, M. S., & Cook, R. G. (2008). Absolute and relational control of a sequential auditory discrimination by pigeons (*Columba livia*). *Behavioural Processes*, *77*(2), 210-222.
- Nelson, B. S. (2000). Avian dependence on sound pressure level as an auditory distance cue. *Animal Behaviour*, *59*, 57-67.
- Nelson, D. A. (1988). Feature weighting in species song recognition by the field sparrow (*Spizella pusilla*). *Behaviour*, *106*(1/2), pp. 158-182.
- Park, T. J., & Dooling, R. J. (1985). Perception of species-specific contact calls by budgerigars (*Melopsittacus undulatus*). *Journal of Comparative Psychology*, *99*(4), 391-402.

- Parton, S., Yelda, S., Price, V., & Shimizu, T. (2005). Female pigeons, *Columba livia*, respond to audio/visual playbacks of male courtship behavior. *Animal Behaviour*, *70*, 957-966.
- Porter, D., & Neuringer, A. (1984). Music discriminations by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, *10*(2), 138-148.
- Ralston, J. V., & Herman, L. M. (1995). Perception and generalization of frequency contours by a bottlenose dolphin (*Tursiops truncatus*). *Journal of Comparative Psychology*, *109*(3), 268-277.
- Saffran, J. R., & Griepentrog, G. J. (2001). Absolute pitch in infant auditory learning: Evidence for developmental reorganization. *Developmental Psychology*, *37*(1), 74-85.
- Striedter, G. F. (1994). The vocal control pathways in budgerigars differ from those in songbirds. *The Journal of Comparative Neurology*, *343*(1), 35-56.
- Stokes, D. W., & Lansdowne, J. F. (1979). *A Guide to Bird Behavior*. Boston: Little, Brown.
- Trehub, S. E., Bull, D., & Thorpe, L. A. (1984). Infants' perception of melodies: The role of melodic contour. *Child Development*, *55*(3), pp. 821-830.
- Wallschläger, D. (1980). Correlation of song frequency and body weight in passerine birds. *Cellular and Molecular Life Sciences*, *36*(4), 412.
- Weary, D. M. (1991). How great tits use song-note and whole-song features to categorize their songs. *The Auk*, *108*(1), pp. 187-190.
- Wild, J. M. (1994). The auditory-vocal-respiratory axis in birds. *Brain, Behavior, and Evolution*, *44*, 192-209.
- Wild, J. M. (1997). Neural pathways for the control of birdsong production. *Journal of Neurobiology*, *33*(5), 653-670.

Wildenthal, J. L. (1965). Structure in primary song of the mockingbird (*mimus polyglottos*). *The Auk*, 82(2), pp. 161-189.

Williams, H., & Nottebohm, F. (1985). Auditory responses in avian vocal motor neurons: A motor theory for song perception in birds. *Science*, 229(4710), 279-282.

Wit, H. P., Scheurink, A. J. W., & Bleeker, J. D. (1985). Hearing thresholds of normal and fenestrated deaf pigeons. *Acta Otolaryngol*, 100, 36-41.