Detection and Discrimination of Complex Sounds by Pigeons (*Columba livia*)

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Abstract

Auditory scene analysis is the process by which sounds are separated and identified from each other and from the background to make functional auditory objects. One challenge in making these psychological units is that complex sounds often continuously differ in composition over their duration. Here we examined the acoustic basis of complex sound processing in four pigeons by evaluating their performance in an ongoing same/different (S/D) task. This provided an opportunity to investigate avian auditory processing in a non-vocal learning, non-songbird. These pigeons were already successfully discriminating 18.5 s sequences of all different 1.5 s sounds (ABCD . . .) from sequences of one sound repeating (AAAA . . ., BBBB . . ., etc.) in a go/no-go procedure. The stimuli for these same/different sequences consisted of 504 tonal sounds (36 chromatic notes × 14 different instruments), 36 pure tones, and 72 complex sounds. Not all of these sounds were equally effective in supporting S/D discrimination. As identified by a stepwise regression modeling of ten acoustic properties, tonal and complex sounds with intermediate levels of acoustic content tended to support better discrimination. The results suggest that pigeons have the auditory and cognitive capabilities to recognize and group continuously changing sound elements into larger functional units that can serve to differentiate long sequences of same and different sounds.

In humans, the study of the organization of complex sounds into larger units has received considerable attention, especially for the purposes of processing language and the appreciation of music. One rich vein in this area is auditory scene analysis, a set of psychological processes by which humans come to group and separate sounds from the background and from each other to form functional auditory streams and organized auditory "objects" in a "scene" (Bregman, 1994). Bregman proposed several Gestalt-like principles used by humans to parse apart and attend to auditory objects. These principles identify regularities in how humans group and segregate mixed and competing auditory frequency and amplitude information over time.

The complex sounds generated by human and non-human organisms regularly contain a broad range and distribution of frequency and energy information that varies over their durations. Consequently, non-human animals face the same perceptual problems as humans in identifying, grouping, and separating complex sounds in their normal environments. In most animals, however, the important ability to parse and recognize the differences and similarities of sounds, and then organize them into larger groups, is a poorly understood component of how animals process the continuous stream of auditory information in the natural world. A capacity similar to auditory scene analysis would seem especially valuable for birds, because they regularly use complex vocalizations for essential functions ranging from mate attraction to territorial defense (Gill, 1995; Hulse, MacDougall-Shackleton, & Wisniewski, 1997; MacDougall-Shackleton, Hulse, Gentner, & White, 1998; Wisniewski & Hulse, 1997).

In the current article, we take advantage of a same/different (S/D) approach previously developed in our lab (Cook & Brooks, 2009) to investigate how pigeons process long sequences of changing auditory information. Using this task, we examined how different acoustic features in these stimuli contributed to their successful discrimination. Our understanding of visual S/D

concept learning and processing in animals has made substantial progress over the last 20 years (Cook & Wasserman, 2006). Many of these advances can be attributed to the cutting edge research of Edward Wasserman and colleagues within this modality (Brooks & Wasserman, 2008; Castro, Young, & Wasserman, 2006; Cook & Wasserman, 2007; Gibson, Wasserman, & Cook, 2006; Wasserman, Fagot, & Young, 2001; Young & Wasserman, 2001a, 2001b; Young, Wasserman, & Dalrymple, 1997). Advancing our understanding of relational concept learning in animals is just one of his many contributions to the study of comparative cognition. As confirmed by the contents of this special issue in his honor, there is no doubt that his impact has been substantial and widespread. Perhaps a good jumping off point for the current report comes from the notion that "all negative stimuli are not created equal" (Astley & Wasserman, 1992). While that statement specifically concerned the role of similarity within and across perceptual visual categories, we extend that observation here to include how different types of complex sounds also vary in their effectiveness in supporting auditory S/D discrimination.

Given our common interest in relational conceptual behavior using visual stimuli (Cook, 2002; Cook, Cavoto, & Cavoto, 1995; Cook, Katz, & Cavoto, 1997; Cook & Wasserman, 2006, 2007; Gibson et al., 2006; Wasserman, Young, & Cook, 2004), it was a natural to ask whether this type of abstract relational behavior extended to other modalities, like audition (Dooling, Brown, Park, & Okanoya, 1990). As a result, my laboratory began investigating how pigeons discriminate S/D sequences of auditory stimuli (Cook & Brooks, 2009; Murphy & Cook, 2008) as well as other types of auditory discriminations (Brooks & Cook, 2010; Hagmann & Cook, 2010). In the experiments most directly related to the current report, Cook and Brooks (2009) successfully trained pigeons in a go/no-go auditory S/D task in which the animals determined if a sequence of sounds was comprised of a series of different sounds or consisted of a single sound

repeated over time. The pigeons were reinforced for pecking at S+ *different* sequences comprised of 12 randomly-selected sounds, while pecking at S- *same* sequences of one sound repeated 12 times resulted in a variable timeout. Cook and Brooks found that pigeons were able to learn the discrimination with tonal sounds and show generalized transfer to various novel stimuli (e.g., novel pitch/timbre combinations, pitches, instruments, and complex natural and man-made sounds). These results suggested that pigeons can learn generalized S/D concepts outside of their dominant visual modality. Using a different procedural approach, the relational nature of responding to auditory stimuli by pigeons, as well as control by their absolute properties, was also found by Murphy and Cook (2008). What was left unidentified in these studies, however, was the acoustic basis of this relational responding.

All acoustic stimuli are comprised of the summation of disturbances in the transmitting media, and they are frequently considered to be the summation of multiple sinusoidal functions. Pure tones are the simplest of all such stimuli. These consist of only a single sinusoidal wave that is described by a singular frequency and is perceived as a single pitch that does not change perceptually over time. Simple tonal sounds, such as those produced by musical instruments, are a little more complex than pure tones. Each of these contains a fundamental frequency that is the perceived pitch of the tone. Furthermore, there are additional harmonic frequencies that ebb and flow during playback which contribute to the timbre or distinctive sound of each instrument. These tonal sounds may also contain frequency and amplitude changes that cause variation in the perception of the attack or decay of the sound, as well as its possible vibrato. Computers can synthesize tonal sounds played by instruments by modeling the harmonics of the timbre at various frequencies and computing from those models the desired frequencies to generate a

given instrumental sound. The top panel of Figure 1 depicts a single note "played" by a computer-synthesized alto saxophone.

Next on the scale of harmonic intricacy would be various types of complex sounds, such as bird songs or man-made sounds. Complex stimuli are generally both harmonically and temporally more variable, especially since their content may change continuously over their duration. Two examples of such complex sounds are in Figure 1, which shows the spectrograms of a man-made sound and a bird song. One of the challenges in the processing of these more extended complex sounds is to recognize the larger organization and structure of the sounds as they change with time. For instance, is the willet's song experienced as one large, two intermediate, or nine smaller units? Are the overlapping and simultaneous frequencies that start and stop asynchronously in the church bells perceived as a sequence of different tones starting and stopping at odd intervals or just one larger functional grouping?

Given this, consider for a moment a *same* trial in our S/D procedure when composed of a complex sound like the willet's song. In accordance with the training contingencies of our S/D task, the pigeons learn to suppress their pecking when presented with repetitions of a complex sound within a sequence. However, a complex stimulus has multiple frequencies and patterns that constantly change over every moment of its presentation. Thus, why do the pigeons not simply respond "different" to this ever-changing microstructure on *same* trials with complex stimuli? The answer must lie in part that the pigeons can recognize the repetition of the extended pattern of changing frequencies over time by grouping them together into larger representational units of a "sound." Because the momentary perception or statistics of complex sounds are inherently unreliable, the pigeons must be responding to the differences or the repetitions of such larger units when making auditory "same" or "different" responses.

Our ongoing program of auditory S/D research offered us an opportunity to examine this larger issue by evaluating how pigeons processed different complex stimuli and how they did so relative to simpler tonal stimuli. For example, because of their greater momentary differences, would complex sounds be more difficult to discriminate than simpler, more uniform tonal stimuli? Or, perhaps, would any perceptual differences among the sounds be equally sufficient, since all could fill the role of being "same" and "different" in the pigeons' generalized approach to the S/D task?

During the course of conducting other tests and experiments with our S/D experienced pigeons, we had collected an extended set of "baseline" data using a large number of tonal and complex stimuli that had been regularly presented over this period of time. As a consequence, we possessed a large database of S/D performance for each bird that we could draw on to see if and how there were differences among the auditory stimuli. Here, we report the analysis of S/D performance of four pigeons with a wide variety of tonal, natural, and artificial sounds. Further, we examined how a number of different acoustic properties correlated with their ability to recognize the repetition of these sounds. For the latter analyses, we concentrated on their responding on S- *same* trials. We did this because these S- trials have only a single, unambiguous stimulus that requires evaluation (as opposed to the multiple different sounds presented on each *different* trial), and they occurred with a higher frequency than usable positive trials (since S+ responding required evaluating non-reinforced trials that were programmed to occur less frequently).

Specifically, we evaluated how *same* trial performance with 504 tonal stimuli (14 musical instruments; 36 chromatic scale notes) and 72 complex sounds (26 bird sounds; 46 man-made and non-avian animal sounds) co-varied with ten different acoustic properties measured from

each sound. These measurements included average frequency, average amplitude, and total silence-removed sound duration. Several metrics also captured the variation of the sounds over time as metrics of acoustic complexity. These included measures of the number of frequency and amplitude transitions, the overall ascending or descending nature of frequency and amplitude, and the average autocorrelation of the sound with itself. Our desire was to identify those properties leading to the best discrimination of "sameness" within these stimuli. Presumably, understanding how these acoustic properties influenced the relative perception of sameness would provide insight into how the pigeons also determine differences within a sequence.

Method

Animals

Four male pigeons (*Columba livia*) that were highly familiar with the S/D discrimination were tested. Two birds had 82 months of experience prior to the current testing and had served in Cook and Brooks' (2009) experiments, while the other two had 29 months of experience and served previously in Murphy and Cook's (2008) experiments. No consistent differences were found between the lesser and greater-trained pigeons, so this factor was excluded from analysis. Three of the pigeons were maintained at 80-85% of free-feeding weight and the fourth at 85-90% due to his size. All were housed in a standard 12:12 L:D environment in a central colony room.

Apparatus

A flat-black Plexiglas chamber (42.5 cm wide × 44 cm deep × 39.5 cm high) was used for testing. Auditory events were controlled using a computer with a built-in sound card (SoundMax Integrated audio card; Analog Devices). The auditory stimuli were simultaneously presented from two multimedia speakers (earlier Harmon-Kardon HK-195; later Harmon-Kardon CN-02320V) located towards the front of each side of the chamber. These speakers both had a fairly flat frequency response profile over their response range of 80 to 20000 Hz. The speakers were

situated behind plastic grills (a 9.0 × 12.0 cm grid of 5 mm holes) in the sides of the chamber.

Visual stimuli were presented on a color monitor (NEC Accusync LCD 52V; resolution 1024 ×

768) located immediately behind a transparent infrared touch screen (an EloTouch for the first

portion of the observations; an EZ screen touchscreen over the latter) in an opening in the front

panel. A 28 V houselight illuminated the testing area, except during timeouts. Mixed grain was

delivered by a food hopper (Coulbourn Instruments) placed centrally in the front panel below the

touchscreen.

Same/Different Go/No-Go Procedure & Inclusion Criteria

Pigeons were trained using the go/no-go procedure detailed in Cook and Brooks (2009). The

pigeons were required to discriminate between *same* sequences (S- trials), comprised of a

randomly selected sound repeated 12 times in succession, and *different* sequences (S+ trials),

comprised of 12 completely different sounds in a random order (e.g., discriminate AAAA…. or

BBBB…. from ABCD…). The 12 sounds were presented for 1.5 seconds each with 50-ms inter-

stimulus intervals (ISI). Each trial in a session started with the illumination of a 2.5 cm white

ready signal. After a single peck to the ready signal, a purple square (5.5 × 5.5 cm) response area

was displayed centrally on the screen and the auditory stimuli began playing through the two

laterally positioned speakers. Pecks to this purple square during *different* trials were reinforced

while pecks to it on *same* trials resulted in a variable timeout after the trial. Pecking on *different*

trials was reinforced with 2.8 s access to grain on a variable interval (VI) schedule (this was

increased to 6 s for one bird in order to maintain weight). The sound sequence continued to

advance and play during any within-trial reinforcements. Two pigeons were reinforced on a VI-8

schedule, but the other two pigeons were reinforced on a shorter VI-5 to maintain peck rates and

weight. A small percentage of *different* sequences were regularly tested as probe trials in which

no food reinforcement was permitted. These unreinforced probe different trials allowed for the

uncontaminated measurement of peck rate without the direct cues associated with reinforcement and the missed time pecking the display that occurred while eating from the hopper. Analyses of *different* trials only used data from these probe trials. After the auditory sequence ended, the purple response area was removed. On S- trials this was followed by a dark timeout proportional to the amount of pecking that occurred on that trial. This was followed by a 5-s inter-trial interval (ITI) and then the next trial's ready signal being displayed.

To examine the factors behind the birds' ability to discriminate different kinds of sounds, ongoing baseline trials from the training and test sessions conducted over a 34-month period were harvested and examined. During this period of time, the pigeons participated in a series of experiments focused on different aspects of S/D or auditory processing. At the core of each of these sessions were a set of baseline trials that were continually tested over this time period. We used these baseline trials to build the dataset analyzed here. We identified 700 sessions for each bird (eliminating partial or otherwise corrupted sessions). We then excluded any test or control trials associated with the various experiments. These omitted experimental trials focused on how the pigeons' discrimination transferred to specific stimuli (i.e. novel timbres, pitch ranges, different organizations of trials, etc.). Virtually all were tested as non-reinforced probes. Otherwise, from these sessions, we collected the following baseline conditions of *same* and *different* trials: 1.) Pitch-only tonal trials (typically 10 or 12 trials per session, although this varied over some of the sessions) consisting of randomly selected different or same notes from the same instrument. 2.) Timbre-only tonal trials (10 or 12 trials per session) consisting of randomly selected different or same instruments playing the same note. 3.) Complex sound trials (12 to 24 trials per session), consisting of randomly selected different or same sounds from a library of animal (non-birds) and man-made sounds. 4.) Bird song trials (10 or 12 trials per

session), consisting of randomly selected different or same bird songs or calls from a library of such sounds. 5.) Pure tone trials (10 or 12 trials per session) consisting of randomly selected different or same pure tones. This resulted in a collection of approximately 19,000 same trials and 4,800 different trials per bird for analysis.

Auditory Stimuli

Auditory stimuli were presented by the computer using 1.5 s WAV files. These were played at between 76-85 dB as measured from the bird's typical position in the chamber (Radio Shack sound pressure meter; Weighting A, fast response). Tonal stimuli were software-generated, synthesized waveforms (Sonar Cakewalk, Boston, MA) sampled at 44.1 kHz and stored as 16 bit sound files. The tonal stimuli consisted of 36 pitch values using a standard chromatic scale starting on C (fundamental frequency range = 65-523 Hz). This range is one octave lower than reported in Cook & Brooks (2009), despite the fact that both reports use the same stimuli. The previous report's mistake in the reported range resulted from a misunderstanding of how the note notation system used by SONAR relates to that typically used by musicians. The tonal sounds were synthesized as played by 14 simulated musical instruments (piano, guitar, vibraphone, reed organ, violin, harmonica, alto sax, oboe, trumpet, French horn, flute, clarinet, cello, and organ). These 504 tonal stimuli were used to construct the pitch-only and timbre-only conditions.

A total of 72 non-tonal complex sounds were available for analysis. The 46 complex sounds used in the *complex sound* condition were a combination of 10 non-avian animal sounds and 36 man-made sounds and came from CD-ROM or Internet collections. The 26 bird songs or calls in the *bird song* condition were from field recordings of birds that were also obtained from CD-ROM and Internet sources. These sounds were selected to have durations and natural phrasing that fit within the 1.5 s presentation time, but were not otherwise standardized. Because of their different sources, these sounds varied in sample rate between 8 and 44 kHz with bit depths of

either 8 or 16 bits and could be either mono or stereo. Complex and bird song conditions were not mixed within a sequence.

Acoustic Analysis

Information about the harmonic and amplitude structure of these sounds was measured using a bioacoustical analysis program (SIGNAL 5, Engineering Design, Berkeley, CA). Ten acoustic properties were selected as representative of the sounds. These properties included:

Sound duration: In order to measure the duration of sound with the inter-element silence removed, it was necessary to determine what level of sound was audible and then evaluate how much of the playback exceeded that threshold. A limited number of the complex sounds had some audible low-volume, high-frequency noise as part of their recording, rendering absolute metrics unreliable. To accommodate these features, sound duration was measured as the total amount of time a sound's volume was measured to be within 40 dB of its maximum amplitude.

Average frequency: This was calculated using SIGNAL's default method for average frequency. This property considered only those portions of the sound that had audible content (i.e., silence did not lower the value of this metric).

Peak frequency: This was computed using the Fourier analysis of the signal, which calculates the relative contribution of each frequency in the sound. The Fourier analysis was computed with 8192 bins using a Hann window. The frequency bin with the most power was considered the peak frequency.

For our remaining frequency-based analyses, the dominant frequency contour of the sound (i.e., the spectral contour) was calculated using SIGNAL's Spectrogram Contour Detection algorithm. The spectral contour function was computed by using frequencies above an amplitude cutoff at 40 dB below the signal maximum and continuing over the 1.5 s time course of the sound to find adjacent dominant frequencies. This provided a shape that traced the dominant

pitch over the sound's progress. Similarly, an amplitude envelope was derived for the purposes of analysis. To obtain the amplitude envelope, the intensity of the original waveform was converted to all positive values. The envelope followed the rise of the original waveform equation identically, but never dropped below a predetermined exponential rate based on the signal bandwidth. This predetermined rate allowed the envelope to have a continuous form that ignored small sinusoidal variations over small gaps. Using this transformed information we computed:

Frequency bandwidth: This was the difference or range between the maximum and minimum frequency values of spectral contour. The final value represented the frequency range in Hertz above the aforementioned amplitude threshold.

Number of frequency transitions: This represents the number of times the spectral contour changed from ascending to descending over the course of the sound on a sample-by-sample basis (i.e., using a minimum run length of 1) without a "just noticeable difference" threshold applied (i.e., all changes in frequency were considered transitions).

Ascending frequency score: This represents an additive value of the number of samples in which the spectral contour was rising in frequency minus the number of samples in which the frequency fell. This was also evaluated on a sample-by-sample basis without a threshold. The final value represents roughly the amount of time a sound's contour spent ascending. Negative values indicate a net descent in frequency.

Average amplitude, *number of amplitude transitions* and *ascending amplitude score* correspond to the same calculations as done in the frequency domain, but using the amplitude envelope described above. Again, this was evaluated on a sample-by-sample basis without a threshold.

Autocorrelation consisted of a cross-correlation run on the same sound. One copy of the sound was kept at a constant point in time and compared with a copy at variable time offsets. This produced a curve that gave the correlation of a sound with itself as a function of time offset. The area under this curve was used as a metric of internal repetition.

In order to analyze the effect of these acoustic properties, we used an AIC-based stepwise method (R function *stepAIC*) to remove predictors based on how well the combination of metrics predicted pecking in a linear mixed-effects model (Pinheiro, Bates, DebRoy, Sarkar, & R Development Core Team, 2013; R Core Team, 2013; Venables & Ripley, 2002). Using results from only *same* trials, we attempted to determine which acoustic properties or features supported peck suppression. This procedure first started by using a complete model (i.e., all predictors were included) with a random effect of bird (R function *lme,* using the maximum likelihood estimation method), with successive removals of single terms as long as removing the term decreased the model complexity as measured by the Akaike Information Criterion (AIC). AIC is a widely accepted measure of how well a model fits a given set of data. Critical for the purpose of multiple regression, it simultaneously reflects how well the model fits the data (i.e., similar to R^2) while penalizing unnecessary complexity caused by an excess of predictors. Thus, by finding the model that minimizes AIC, we can eliminate predictors without sacrificing the model fit, and this method preserves the power in the model for the estimation of model parameters. Every predictor in the final model, however, is not guaranteed to meet the traditional requirements of significance in the linear regression. Therefore, after minimizing AIC, we examine the associated *p* values to determine which predictors make *significant* contributions, in the traditional sense of the term. The *non-significant* predictors usually approach a significant *p* value, but ultimately make more minor contributions to the overall model.

Results

Because of their familiarity with the S/D discrimination prior to these observations, all four pigeons were readily discriminating *same* sequences from *different* sequences at the beginning of the data collection period. The birds were generally stable in their reactions relative to the different conditions examined here. Because the birds differed in their absolute level of pecking in the task, we normalized the data relative to each bird's average peck rate on all included S+ trials.

Figure 2 shows the mean normalized peck rates for the four pigeons for *same* and *different* sequences of pure tones, tonal sounds (pitch and timbre), and complex sounds (complex sounds and bird song) as a function of the serial position of the sound items across a trial. The diverging peck rate functions for the *same* and probe *different* sequences reflect successful go/no-go discrimination (note that since "same" and "different" cannot be determined from a single presentation, peck rates during the first item were equal and have been omitted). For both *same* and *different* sequences, peck rates started out high at the beginning of the sequence. For S+ *different* sequences, these rates remained high across all subsequent sounds, which maximizes the likelihood of reinforcement on the VI schedule.

For the S- *same* sequences, in contrast, the peck rates decreased gradually as repetitions of the "same" sound were experienced. Thus, at least as evidenced in peck rate after the first sound, the pigeons needed several additional playbacks of the sound to recognize its repetition. To examine this for each bird individually, we calculated the point in the sequence when pecking to *same* and *different* sequences significantly diverged as averaged across all sound types. Using 14 50-session blocks for each bird to compute repeated-measures t-tests, we found that two birds significantly differed by the third item (ts(13) > 2.4, ps < .031, d_zs > 0.28; an alpha level of p < .05 was used for all analyses), one bird differed at the fourth (t(13) = 4.6, p < .001, d_z = 1.5), and

one bird by the fifth ($t(13) = 4.4$, $p < .001$, $d_z = 0.87$). Thus, the pigeons on average needed about three sound repetitions (fourth serial position) in S- *same* sequences to significantly reduce their peck rate from the S+ *different* peck rates.

To better understand how peck rate decreased on same trials, we next used SigmaPlot's fit utility to model several types of mathematical functions to these curves. Prior to curve fitting, we translated the data two serial positions to the left, allowing the intercept term to reflect peck rates during the second serial position. This modeling revealed excellent fits for both the two-parameter exponential and the three-parameter logistic functions for the set of S- conditions shown in Figure 2 ($R^2 > .99$). Both mathematical models feature an A parameter, representing the peck rate at the beginning of the sequence, and a B parameter that controls the rate of suppression. The three-parameter logistic also includes an x_0 parameter that reflects the horizontal locus of suppression. When modeling the three parameter logistic ($Y = \frac{A}{1+\left(\frac{x}{x_0}\right)^B}$),

parameters A and B were held in common across the five sound conditions shown in Figure 2, while the x_0 was allowed to vary between these conditions. This resulted in a set of seven total parameters that explained 99.6% of the variation in the curves (A = .99, B = 1.4, x_0 within [5.0, 7.3]). This model would suggest that the birds are engaging in the same behavior in all conditions, with the control of fit by the x_0 parameter suggesting that the speed of detecting sameness differs across conditions. The two parameter exponential ($Y = A \cdot e^{-B \cdot x}$) was modeled similarly, except that A was held fixed while B was allowed to vary between the sound conditions (i.e., 6 total parameters). This function also fit extremely well ($R^2 = .993$; A = 1.01, B within [0.095, 0.116]). This model, as controlled by the fit of the B parameter, would suggest instead that the sound conditions in fact differ in the rate of suppression.

Visually examining the different sound conditions in Figure 2 suggests that complex sound sequences generally supported better discrimination than the pitch or timbre conditions. This pattern was true for three of the four pigeons. To examine differences among the conditions (pitch, timbre, pure tones, bird song, complex), we focused on peck rates over the last six presentations in each sequence, because this captured the pigeons' S/D discrimination at its peak. We analyzed the data using a repeated measures (RM) ANOVA (two S/D × two 350-session blocks × five sound type). This unsurprisingly confirmed a significant difference in peck rate to the same and difference sequences ($F(1, 3) = 11.3$, $p = .044$, $\eta^2_p = 0.79$). It also revealed a significant three-way interaction ($F(4, 12) = 3.4$, $p = .043$, $\eta^2_p = 0.53$). Examining the data revealed that the interaction reflected a relative improvement in discrimination of the tonal stimuli between the first and second half of the data collection period. Thus, over the first portion of testing, performance with tonal stimuli was not as good as with complex stimuli, but this difference disappeared with time. We confirmed this by conducting four additional RM ANOVAs, one for each combination of *same*/*different* and each half of the data collection period. Peck rates during *different* sequences were high and equivalent for all sound types, with the RM ANOVAs indicating no significant main effects of sound condition in either half of the data collection period. For *same* trial responding, however, we did find a significant main effect of sound condition ($F(4, 12) = 3.9$, $p = .03$, $\eta^2_p = .55$) for the first half of the data collection period, but not the second ($F(4, 12) = 1.7$, $p = .223$). The effect in the first half of the data collection period appeared to reflect slightly better suppression with complex and bird song conditions compared to the pure tone or tonal stimuli. During the second half of the data collection period, the pigeons were equally good with each of these sound conditions.

The remaining analyses focused on the pigeons' performance with the 504 tonal and 72 complex sounds and their possible co-variation with the different measured acoustic properties. For this, we examined just S- *same* sequences and the peck rates over the last half or six items of each these trials. First, we examined the tonal sequences. Because the *same* sequences for pitch and timbre trials are perceptually identical – a single chromatic note played using a single musical instrument – we combined the results from these two conditions.

We first separately examined the pitch and timbre properties of these trials, Figure 3 shows how these two major properties affected the pigeons' normalized peck rates over the last six presentations of these *same* sequences. The top panel shows the effect of varying the fundamental frequency across the different musical instruments. Over the three octave range tested here, the pigeons were generally, but only slightly, better at suppressing peck rates to *same* trials that had a higher fundamental frequency. The bottom panel shows the effect of varying the timbre of musical instrument, in sorted order, as averaged across fundamental frequency. The synthesized trumpet and alto saxophone supported better discrimination, and the electric guitar, vibraphone, flute, and piano were the least effective in suppressing peck rate. It is perhaps notable that the least effective instruments generally have an initial attack before tapering in amplitude over their duration, while the more effective tonal sounds were maintained by instruments with clearer and more continuous qualities over their duration. A split-half correlation for each bird revealed that the relative performance with the individual items was stable across the halves of the experiment (tonal rs > .14, ts(502) > 3.1, ps < .002), even if tonal performance overall improved.

We next examined the agreement among the birds about the ranking of fundamental frequency and timbre within these stimuli. This was done by a series of Pearson correlations on

the peck rates between every pairwise comparison of all four birds. For fundamental frequency, the average correlation across all four pigeons was .38 ($r(34)$, range .25- .62). Three of these six correlations were significantly above chance (all three of the non-significant correlations involved a single bird, suggesting that this animal may not have reacted to pitch in the same way as the others). These middling correlations may be lower than expected in part due to the excellent suppression observed across the whole frequency range for each bird. For timbre, the average correlation for all four pigeons was .78 ($r(12)$, range .53 - .92). Five of these six correlations were significantly above chance (the sixth was $p = .051$). Thus, in contrast to fundamental frequency, the pigeons strongly agreed as to which were the better and poorer timbres. These correlations were further confirmed using the AIC-based estimation method to test and remove these two possible predictors (timbre, fundamental frequency) from a linear mixed-effects model (with a random effect of subject). Both made significant contributions to the final model: fundamental frequency, $F(1, 1998) = 64.9$, $p < .001$; timbre, $F(13, 1998) = 74.7$, $p < .001$.

We then extended this same mixed-effects AIC modeling to also include the ten acoustic measures as potential predictors of tonal performance. Because our analysis indicated that the tonal discrimination slightly, but significantly, improved over the data collection period, we included the data collection period and its interaction with each of the stimulus factors in the regression analysis. Using the same AIC-based exclusion method, the final model contained significant linear contributions of timbre ($F(13, 4005) = 55.2$, $p < .001$), fundamental frequency, autocorrelation, and number of frequency transitions ($Fs(1, 4005) > 14.6$, $ps < .001$). Also included in the final AIC model were contributions from bandwidth and data collection period, but these did not show the same strength of linear correlation as the four prior factors $Fs(1, 4005)$

< 1. The model also included interaction terms with data collection period. The coefficients suggested that the effects of number of frequency transitions and autocorrelation were reduced with experience (Fs(1, 4005) > 12.9, ps < .001). Based on the direction of the coefficients, the inclusion of the acoustic predictors beyond timbre and fundamental frequency indicated that tonal stimuli having more frequency transitions, lower autocorrelation and narrower bandwidths tended to generally support better suppression. In tonal stimuli, frequency transitions and autocorrelation variation are the result of vibrato-like features in synthesized sound for some instruments; given the interaction with time, these results suggest the pigeons perhaps learned to discount vibrato in their S/D evaluation of these tonal stimuli.

We next conducted a similar analysis of the complex sounds. Shown in Figure 4 is the sorted order of the complex sounds and bird songs as a function of the average number of normalized pecks over the last six presentations within a same sequence. Again, higher ranks depict those sounds to which the pigeons exhibited the best suppression on *same* trials, while lower rankings show less effective suppression. In comparison to mean *different* responding (bird song & complex trials combined), each of the 72 complex stimuli supported significant suppression of *same* responding for two birds. Birds #3N and #4L showed difficulty discriminating some of the complex sounds (#3N more so than #4L), and #4L had a marginal discrimination with one of the bird songs. We again used a series of Pearson correlations to examine the degree to which the individual pigeons agreed with one another on the rank ordering of these stimuli. The average correlation across all four pigeons was .37 (r(70), range .27- .53). All six of these correlations were significantly above chance. These results suggest that all complex sounds are not created equal, but that the pigeons generally agree on which ones are the best and worst.

We again used linear mixed-effects modeling with stepwise AIC reduction to examine the contribution of the ten acoustic metrics in accounting for these differences in the pigeons' peck suppression. We employed the same AIC-based stepwise removal of factors from the full model to determine which acoustic features were most relevant to performance with complex sounds. The final model included several factors. Of these, sound duration, peak frequency, ascending amplitude score, and bandwidth were marked as making significant linear contributions (Fs(1, 277) > 3.9, ps < .047). Also included in the best final AIC model were contributions from average frequency (F(1, 277) = 3.7, p = .056), number of frequency transitions (F(1, 277) = 3.2, p = .076), and autocorrelation, (F(1, 277) = 2.5, p = .12), but these did not show the same strength of linear correlation as the four prior factors. When examining the direction of the coefficients of the significant contributors, peck suppression generally improved with complex sounds having increased durations, lower peak frequencies, lower ascending amplitude scores, and narrower bandwidths.

Discussion

By helping to elucidate the possible mechanisms by which complex auditory stimuli are processed and recognized by a non-songbird, the current results extend our understanding of avian auditory S/D discrimination. First, the pigeons needed approximately four successive presentations to reliably discriminate *same* from *different* sequences of sounds (although peck rates began to possibly diverge by the end of the second sound). This suggests that auditory processing, control, or decision making is likely slower than in visual S/D processing where the second item regularly supports discrimination (Cook, Kelly, & Katz, 2003). The rate of behavioral suppression across sound repetitions on *same* trials was well fit by both logistic and exponential functions across all sound conditions. Across sound conditions, there may have been an early, small S/D advantage for complex stimuli, but this disappeared with continued training

and testing as the pigeons possibly learned to accommodate the vibrato in the tonal stimuli. Within the different sound conditions, however, not all sounds were equally good at controlling behavior. Sounds with intermediate levels of acoustic complexity generally supported better discrimination of *same* sequences than those that were devoid of auditory structure or pure tones. For tonal stimuli, fundamental frequency and timbre made important significant contributions to a regression-based model of the birds' peck rate with the number of frequency transitions, lower autocorrelation and narrower bandwidths also being factors. For complex sounds, total sound duration, ascending amplitude score, peak frequency, and narrow bandwidths made larger contributions to the final model, with average frequency, number of frequency transitions, and degree of autocorrelation also improving the fit.

Taking these different acoustic analyses together, it appears that pigeons are best at detecting repeated sounds that tend to have intermediate levels of acoustic content over extended durations. Total sound duration was an important factor in the recognition of sameness in the complex sounds. For tonal stimuli, the poorest musical timbres were from instruments with a struck or plucked nature (piano, guitar, and vibraphone). This suggests that sounds having greater total sound energy were generally better for the pigeons. Overall, longer complex sounds would likely have more features within them to support successive comparisons, which makes recognition of their repetition perhaps easier over time. That tonal sounds with lower autocorrelation values also seemed to support better suppression suggests that having more variation of acoustic properties across time is possibly valuable. Such findings suggest that some degree of acoustic complexity can be beneficial. That said, there may be limits to this statement. That sounds with narrower frequency bandwidths and lower ascending amplitude score also tended to support better suppression suggests that acoustic simplicity also has merit and value,

perhaps by limiting the number of auditory features available for attention. Alternatively, since the auditory modality is not the dominant modality, perhaps too much complexity overwhelms the pigeons' auditory processing capacity. The safest conclusion appears to be that pigeons do best at recognizing the repetition of sounds of intermediate acoustic complexity, with too much or too little variation making it more difficult. Difficulty here is a relative term, of course, as the pigeons did not, except for a mere handful of complex stimuli, really find this auditory S/D discrimination particularly hard.

It bears reiterating that these conclusions are limited to the detection of acoustic repetition by the pigeons and not to overall S/D discrimination more generally. Our acoustic analyses only capture differences as related to the perception of sameness. The birds performed well at discriminating all of the sounds and sound conditions, showing clear differences between their *same* and *different* sequences. It certainly seems a reasonable extension to suggest that those acoustic qualities that enhance sameness detection might also contribute to the detection of *different* sequences. Further, at the moment, we just have evidence of a correlation with these auditory features. In order to strengthen these conclusions, experimental manipulation and evaluation is warranted. Since the sessions analyzed here, for example, we have started to collect information from *different* sequences involving just the alternation of two sounds. These two-sound trials will permit us to conduct more refined analyses of how sound statistics are used to recognize the acoustic, perceptual, and conceptual aspects of different sounds.

Of greatest similarity to the current work is the literature on sound discrimination and categorization by budgerigars and several other species using a contrasting same/different approach (Dooling, Brown, Klump, & Okanoya, 1992; Dooling et al., 1990; Park & Dooling, 1985). Dooling and his colleagues have evidence that several species of birds can categorize

complex stimuli from natural calls to snippets of human speech based on their overall similarity. Testing a variety of complex stimuli, their approach has emphasized the detection of difference, as each test trial is poised against a background repetition of a sound. Thus, their method isolates how birds recognize change or difference, whereas our approach isolates the effect of repetition. Another contrast is that the stimuli in their experiments had durations of less than 500 ms (contact calls, human phonemes, etc.) as opposed to the longer 1500 ms durations tested here. While this has the benefits of greater control and simpler analysis, these shorter duration stimuli would not require the same degree or extent of grouping required by the longer complex sounds from the current investigation. Depending on how the *different* sequences were perceived and the current analysis of "same" responding, it would appear that pigeons can appreciate the serial content of auditory information over at least several seconds of time within a sound and across multiple repetitions of it. Thus, the auditory world available for any putative "scene analysis" by pigeons likely extends at least several seconds into the past.

The time course of processing in these sequential auditory presentations can be contrasted with those for sequential visual presentations. Both Cook, Kelly, and Katz (2003) and Cook and Blaisdell (2006) reported functions that show S/D discrimination well under way by the end of the second picture. The birds here seemed to take longer and needed to hear more items to show a comparable level of discrimination (also true in Cook & Brooks, 2009). Neither of the previous visual studies, however, exactly matches the auditory discrimination tested here. In those experiments, the pigeons were trained to peck during *same* sequences and to suppress pecking during *different* sequences, and both experiments used alternating stimuli for *different* sequences during training. Bearing these differences in mind, we believe these differences do not stem from cognitive differences between the S/D concepts generated by visual or auditory stimuli. As it is

not their primary modality, it is possible pigeons may find the auditory discrimination more difficult to process. Alternatively, however, the differences may stem from the fundamental differences in the nature of vision and audition. Visual stimuli afford rapid parallel processing, while auditory stimuli are serial in nature as they unfold over time. It always takes time to listen. As a result, the pigeons may need to attend longer to the auditory sequences in order to extract the relevant information. While, pigeons have a reputation for being difficult to train with auditory stimuli, our experience is that this is not the case. The current results indicate that the meaningful comparison between the cognition and perception related to the processing of these two modalities is feasible.

We see three possible mechanisms by which the pigeons could have discriminated the repetition of the various specific complex sounds. The first mechanism is similar to the notion of an auditory object. Here the microstructure of the sounds is integrated by the auditory system into a functional unit that has a clear beginning and end (i.e., it has object boundaries) and has an internal structure and contour. This "grouping" account aligns with our intuition of what distinct sounds are like. Thus, complex sounds are heard as singular units or events, despite their internal variation and microstructure.

A second possible mechanism is one that relies on the recognition of a simpler, invariant feature that is extracted from each sound. In this case, the whole sound is not necessarily getting integrated, just a portion of it or a local feature. Here what gets compared across repetitions is a particular pitch transition, or other partial segment or part of the sound that is distinctive. This would be like recognizing a baseball game from just the characteristic "crack" of the bat. Despite its other merits, the regression approach used here would likely miss such feature-based contributions. Since the identity of such distinct features could be different, idiosyncratic, or

unique for each complex sound, the more global modeling approach used here would not detect such local features, unless they were captured by our global metrics and are used across many stimuli by most birds. Perhaps a finer local analysis of the psychological features within the complex sounds in conjunction with inter-sound comparisons could isolate evidence for this approach.

Finally, a third alternative is that the birds might also capture the "gist" of each sound. This is a relatively new idea as applied to audition, but for some time there has been discussion of the visual system quickly computing the gist of a scene. In this possible mechanism, the pigeon is sensitive to the global or general properties of the sound overall without necessarily encoding all of its temporal structure or variation. This capture of a complex sound's general properties rather than its detailed properties could be sufficient to account for most of the effects reported here. For example, even with complex sounds, the birds may extract the general harmonic content of such a sound by which they can easily compare it with the same global properties of the next sound (e.g., overall frequency is changing or not).

At the moment, it is hard to distinguish among these three different alternatives for the grouping of individual sounds and long sequences of sounds. Examples that many birds can potentially recognize and group together longer phrases into "objects" seem to be abundant in nature. Mate attraction, individual recognition and territorial defense often rely on being able to detect the same "song" as it is repeated (Gill, 1995). Winter wrens, for example, string together long songs over many seconds to advertise for mates (Kroodsma, 1980). Over the years, considerable effort has gone into identifying the key features for such recognition (e.g., Emlen, 1972; Nelson, 1989). Reversing the sequence of sounds is known to interfere with recognition of some songs, suggesting that the processing of auditory sounds produces temporally organized

units (e.g., McCasland & Konishi, 1981). Future research will need to delve further into how pigeons and other birds can integrate and parse such complex sounds into larger representational units that can function to support both laboratory and natural discriminations.

It has been suggested that birds are especially adapted to best discriminate their own conspecific vocalizations. Pigeons, however, do not appear to have highly specialized brain regions for conspecific processing, perhaps not surprising given their limited vocal repertoire. Nonetheless these birds apparently are equipped to deal with a large and complex acoustic world, one that is at least sufficient to deal with the number of bird songs and calls tested and discriminated here. Whether they heard those as something of larger relevance or just a collection of sounds is, of course, unknown. Certainly the bird songs were not markedly different to the other sounds in how well the pigeons performed with them. Perhaps, a songbird of some type would have been much better at this S/D task with such stimuli. What is clear is that the widespread reputation that pigeons are acoustically challenged as a consequence of their not emitting complex "song" or learning their vocalizations is not particularly merited. Rather it appears that pigeons are far better equipped to deal with a complex sonic world than previously suspected.

Finally, it is worth a comment as to the meaning of the current results for the possibilities that animals can appreciate human music (e.g., Porter & Neuringer, 1984). One implication of the current study is that pigeons have at least the capacity to integrate and hear complex sounds and distinguish sequences of complex sounds, and as a result, they could conceivably hear a "melody" from a series of notes. When combined with their ability to distinguish among the harmonic content of different chords, the melodic and harmonic competencies for hearing music might be present (Brooks & Cook, 2010). That said, we have found little evidence that suggests

that pigeons, unlike some parrots, can appreciate any of the rhythmic components, except perhaps simple tempo (Hagmann & Cook, 2010; Patel, 2008; Patel, Iversen, Bregman, & Schulz, 2009). While "two out of three ain't bad", without being able to integrate all three of these essential musical components, any appreciation of the larger configural organization of music seems beyond the auditory and cognitive abilities of this particular species (Fitch, 2013).

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Author Notes

Figure Captions

Figure 1. Spectrograms of sample stimuli from the tonal, complex, and bird song sound conditions tested in the experiment. Within each panel, the horizontal axis depicts the 1.5 s duration of sound. The vertical axis indicates frequency in kHz, and the darkness of a region within the plot indicates the power in each frequency at that time.

Figure 2. Peck rates over the presentation of successive sound items in a trial. The five sound conditions are depicted using different colors, and the positive or negative assignment of the trial is indicated by the fill. All pecks were first standardized for each bird to the average S+ peck rate at 1.0 normalized pecks per bin. Responses to the first item are not shown, since the S/D discrimination commences only with the onset of the second item.

Figure 3. Mean normalized peck rates over the last six items on *same* sequences as a function of the different properties of tonal stimuli (pitch and timbre). The top panel shows peck rate as a function of the 36 fundamental frequencies averaged over the 14 musical instruments tested as well as pure tones. The bottom panel shows the sorted rank ordering for how well the pigeons suppressed on *same* sequences to the 14 musical timbres and the pure tone condition averaged over chromatic note. In both of these panels, lower values indicate better suppression (i.e., good same performance). Error bars depict standard error.

Figure 4. Sorted rank ordering for the complex sounds and bird songs as a function of the mean number of normalized pecks over the last six presentations in *same* sequences. The different bar colors indicate exemplars from these two sound conditions. Lower values indicate better suppression (i.e., good same performance). Error bars depict standard error.