

Auditory “Object” perception in pigeons (*Columba livia*)

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Abstract

Separating auditory signal from noise is necessary for survival (e.g., discerning a hawk’s cry from a brook’s roar). Previous research suggests that auditory object perception is based on temporal features of a single stimulus and across the auditory stimuli within close temporal proximity (i.e., trial). To understand time’s influence on auditory grouping, pigeons were tested in an auditory same-different go/no-go task. Pigeons were trained to peck if sounds in a series were different (S +) and suppress pecks if a sound repeated (S -). Experiment 1 varied the sound’s presentation rate and revealed that pigeons did not change their peck rates when the tempo changed. Experiment 2 changed the local sequence by presenting the same sounds forward and reversed, but found no change to discrimination. Experiment 3 divided sounds into equal parts and scrambled the parts to create a new order. Scrambling had no effect on discrimination. These results suggest pigeons use one or multiple time-invariant auditory features to solve a same-different discrimination.

Keywords: pigeon, auditory, temporal processing, grouping, auditory scene analysis

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Introduction

The visual system’s ability to take many small, local features and combine them to form a larger, more global visual object is described through Gestalt psychology. For instance, instead of attending to an individual eye on a face, we instead look at both eyes, the nose, mouth, and the shape of the face as well as how those local features are organized within in the global face. Gestalt psychology posits several heuristics or laws that describe how we form these larger visual groups or objects (e.g., how we form a face; Wagemans et al., 2012). These heuristics describe how humans perceive the visual world, but have been experimentally demonstrated in other animal species, especially avian species (e.g., starlings can discriminate between random dot patterns and dots that form concentric circles; for a review see Cook, Qadri, and Keller (2015)). Visual perception studies frequently attempt to understand how humans and animals form these global objects. What heuristics do we use to form the visual object of a face? One common way researchers try to study these phenomenon is by presenting a visually disrupted stimulus. The ease of disrupting an image, or even a sound, can tell you a lot about what the psychological glue or rule is that stuck it together, as well as the strength of that rule.

Cerella (1980) presented a well-known visual object disruption study where he trained two pigeons to discriminate Charlie Brown from the various other *Peanuts* characters (Cerella, 1980). Then on transfer, Cerella (1980) reorganized the different parts of Charlie Brown’s body (e.g., legs above the torso and the head at the bottom). The goal of this experiment was to determine whether pigeons could still recognize Charlie Brown when his global features were no longer congruent with training. If they were still able to select Charlie Brown over the other characters, they must be using some local features to discriminate, not the global Charlie Brown. After splitting Charlie Brown into three sections (i.e., head, torso, and legs) and scrambling those

sections the pigeons responded equally to the unscrambled Charlie Brown as they did to the scrambled Charlie Brown. It was concluded that pigeons, at least visually, use the local features of stimuli as opposed to the global features when making visual discriminations.

In the same vein, Kirkpatrick-Steger, Wasserman, and Biederman (1998) also rearranged visual stimuli. They tested how scrambling parts of objects, line drawings of human-made items, affected pigeons’ recognition of well-trained stimuli. The results showed that disrupting the ways different parts of objects interconnect with one another had the most profound effect on the visual object recognition. Numerous other studies have also demonstrated the effects of scrambling features on visual object recognition and perception (e.g., Aust & Huber, 2001, 2003; Kirkpatrick-Steger et al., 1998; Kirkpatrick, 2001). Scrambling in the visual domain offers insights about our visual perception, but can scrambling similarly offer information about the structure in other modalities? Animals receive input from many other modalities.

Auditory scene analysis is the auditory equivalent to Gestalt psychology. It posits laws or rules to explain how humans form auditory “objects,” or groupings of local features (Bregman, 1994). Auditory scene analysis (ASA) involves a listener grouping auditory stimuli into a more complex “object” that has distinct boundaries and is recognizable as a standalone unit (e.g., distinguishing the sound of your alarm clock from the noise of your roommate’s snoring or the shower running). It has been studied extensively in humans, increasing our knowledge of how people perceive auditory stimuli by introducing concepts such as auditory stream segregation (A.S. Bregman & Campbell, 1971) and grouping by both spatial and temporal proximity (e.g., Tougas & Bregman, 1985, 1990). While ASA was postulated to explain human auditory perception, other animal species must also use a similar process to navigate their auditory world. To avoid predation, communicate with conspecifics, and for mating behaviors (e.g., a female

finch bird discriminating a male finch’s song during the dawn chorus; Hulse, MacDougall-Shackleton, & Wisniewski, 1997), animals must separate signal (e.g., a song) from the noise in their environments.

There are two reasons for studying any species, the specialist approach or the generalist approach. In the specialist approach, a species is studied because it is an expert in the research topic or skill one is interested in (e.g., studying audition in a black-capped chickadee). Conversely, the generalist approach takes a non-expert species and examines their abilities across a wide array of topics to better understand that species and how its’ abilities compare to other species’. The specialist approach examines what aspects of discrimination make the animal superior to non-specialist species while the generalist approach determines what a generalist species can do despite not having specialized brain regions for specific skills. In the current experiment, we take a generalist species, the pigeon, and attempt to learn more about its’ auditory cognition and perception. Pigeon visual perception has commonly been examined across a variety of cognitive studies (Cerella, 1980; Cook et al., 2015; Kirkpatrick, 2001) due to their versatility in the lab and the ease of data collection. Our vast knowledge on pigeon cognition broadly, is yet another advantage to studying pigeons. While pigeons are not vocal learners (i.e., they do not learn and communicate through song, like songbirds), there have been published studies on their auditory perception using simple pitch and timber stimuli (Brooks & Cook, 2010; Cook & Brooks, 2009; Murphy & Cook, 2008). While there is a basic understanding that pigeons can perceive sounds, next to nothing is known about how they perceive complex auditory structures.

Results from our lab suggest that pigeons can form auditory objects from complex stimuli evidenced by Figure 1A. Here we see that pigeons maintain pecks to a series of 12 unique

auditory stimuli, Different (S+) trial, while they suppress pecks to a repeated series of the same sound, Same (S-) trial. The goal was to see if once trained to distinguish these series of simple stimuli (e.g., pitches), the pigeons could generalize the discrimination to complex stimuli consisting of multiple pitches, timbres, and general auditory features. This would suggest that they could combine auditory features into a single auditory object for each complex sound. The complex stimuli were either 12 natural, man-made sounds (e.g., car horn) or 12 natural bird songs. Pigeons had to suppress pecks to series of repeated sounds (Same trial; S-) and peck at series with 12 distinct sounds (Different trial; S+). As time progressed within a trial, pigeons suppressed pecks to non-reinforced Same (S -) trials while maintaining pecks to reinforced Different (S +) trials (see Figure 1A). Thus, while each sound had multiple local features to potentially attend to, the pigeons could have also formed more global auditory objects to solve the discrimination.

Another study from our lab (Langer, Qadri, Keller, & Cook, *in prep*), examined pigeons' ability to discriminate six-note sequences that either had ascending pitches (i.e., each pitch was a semitone higher than the pitch before) or a descending pitch (i.e., each pitch was a semitone lower) compared to random sequences of the same pitches. This experiment aimed to determine if the pigeons could form auditory objects composed of pitch stimuli in a consistent pattern, ascending or descending, from the same pitches randomly sequenced. If the pigeons could recognize the distinct pattern (e.g., A-B-C-D-E-F) and distinguish it from a random sequence of the pitches (e.g., D-A-E-C-B-F), it would suggest that order mattered to the formation of their auditory objects. Same trials (S-) involved the same repeated six-note sequence, while Different trials (S+) varied the pitch sequence on successive presentations. This experiment was tested across different presentation rates and Langer et al. (*in prep*) found that at faster rates there was a

significant difference between ascending and random sequences. Figure 1B depicts this discrimination at 400 bpm when the discrimination was significant. These results suggested that pigeons need the pitch sequences to be presented above a certain tempo otherwise they were unable to form auditory objects. This finding caused us to ask whether the pigeons were using some global temporal set of features to complete these types of auditory discrimination.

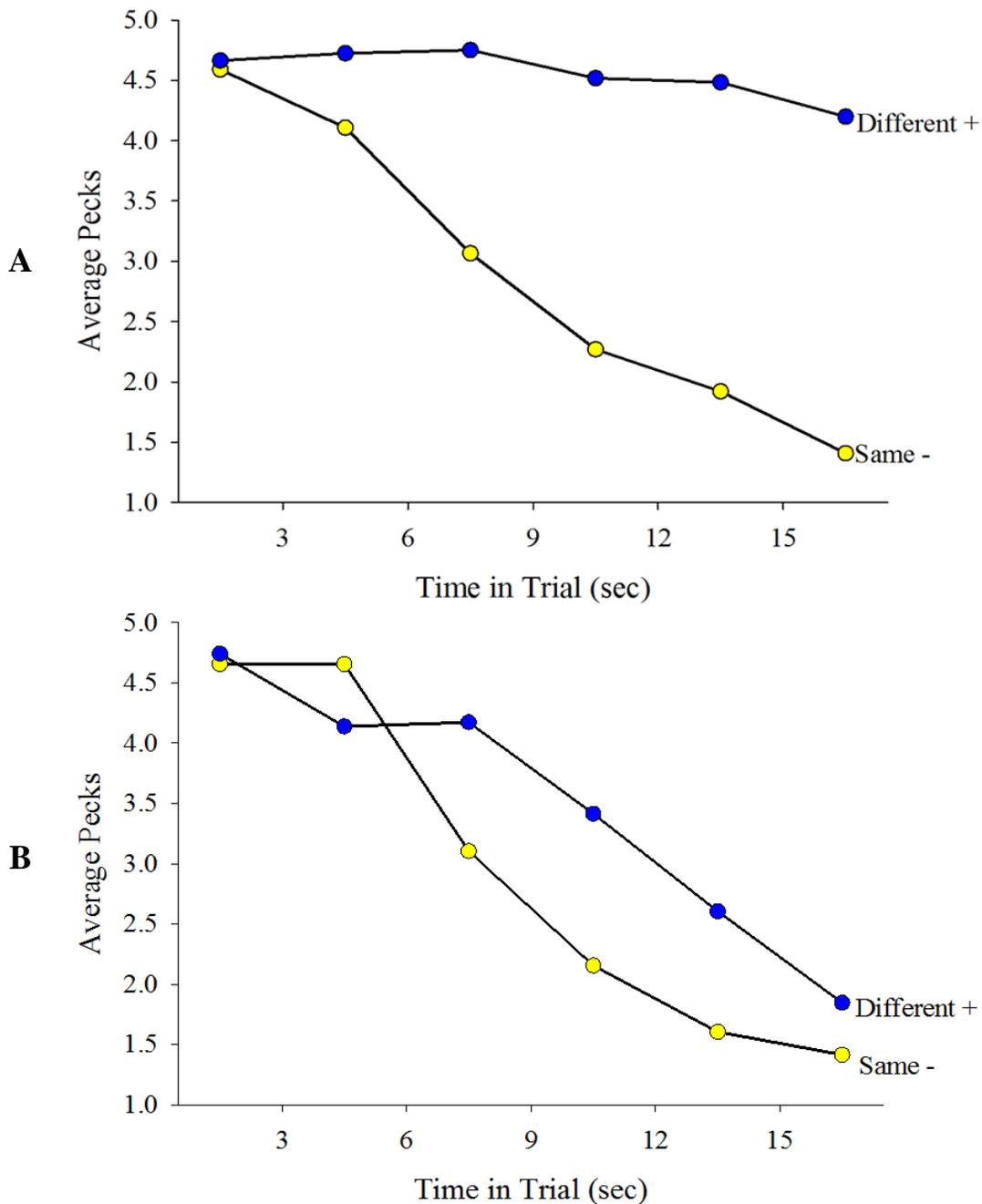


Figure 1. Previous results from our lab with complex stimuli. Panel A depicts pigeons’ abilities to form auditory objects of complex stimuli. Panel B shows the results of rate on auditory object formation for artificial stimuli.

Current Study

Langer, Qadri, Keller, & Cook (*in prep*) tested pigeons with a basic same-different go/no-go task using 12-sound series. Pigeons were trained that pecking at series of 12 distinct complex sounds (Different, S+) would be reinforced, but pecking at series incorporating the same sound repeating 12 times (Same, S-) caused a dark timeout. Unlike static visual stimuli, auditory stimuli necessarily unfold over time, suggesting temporal features would affect perception. With this knowledge, we hypothesized that pigeons use auditory temporal features to form auditory objects; henceforth, known as the Object Hypothesis. If the pigeons are unable to discriminate Different (S+) and Same (S-) trials by suppressing their pecks to S- trials, it would suggest they are not perceiving the individual sounds as distinct objects. We conducted three experiments to test whether pigeons were forming individual sound objects (i.e., each sound was its own distinct object that was compared to the next object in a sequence). Each experiment manipulated a different temporal aspect of the auditory stimulus to investigate the Object hypothesis.

Experiment 1 manipulated the auditory object presentation rate of complex auditory stimuli. The complex stimuli were a mixture of man-made sounds (e.g., a car engine revving) and natural sounds (e.g., a cardinal’s song) and were intended to have diverse auditory features compared to the simple pitch stimuli. In the visual domain, research has shown that presentation rate of sexual behaviors (e.g., strutting) is a sign of vigor and physical condition across many species including sticklebacks, guppies, butterflies, and some bird species (Andersson, 1991; Farr, 1980; Gibson & Bradbury, 1985; Magnus, 1958; Rowland, 1995). Further, birds’ visual courtship displays are more effective at faster tempos (i.e., female birds are more receptive to the

males). We believe that a similar mechanism would be at play within the auditory domain. Birds use auditory signals during courtship; therefore, shouldn't auditory temporal features, such as rate and order, matter to birds? Furthermore, the rate results from Langer et al.'s (*in prep*) examination of tonal sequences suggest that faster rates facilitate grouping.

Experiment 2 changed the local sequence of auditory features in the stimuli by comparing the stimuli played forward and reversed. Songbird playback studies, where a bird's own song is played back to itself, have shown a clear decrease in responding when a song is played reversed compared to when played forward (Goodson & Adkins-Regan, 1997; McCasland & Konishi, 1981). This suggests that the temporal order, or at least how an auditory stimulus starts, can influence whether it is recognized. If the birds group each sound into individual auditory objects that are dependent on the temporal organization of the sound, then playing sounds forward and reversed would lead to the creation of different objects. Finally, Experiment 3 reorganized the sound sequence order similarly to the visual scrambling experiments mentioned previously (e.g., Kirkpatrick-Steger et al., 1998). This will examine whether reorganizing the sound has any impact on their recognition similarly to the visual domain. If the birds perceive each sound in a specific order, then rearranging the order of sound chunks will create multiple objects of the same sound; one for each reorganization of the sound.

Experiment 1: Presentation Rate

Experiment 1 examined the effect of presentation rate on auditory object perception using a previously trained set of simple pitch and complex stimuli. A pilot study with three pigeons presented the same sound at various rates and found no effect of varying the presentation rate on their auditory discrimination. Instead of maintaining pecks to a trial presenting the same sound at varying rates, pigeons suppressed their pecks suggesting they recognized the sameness of the

sounds despite the changing presentation rate. A single trial presented the same sound multiple times and each time the sound was presented it was at the same presentation rate. The results showed no effect of presentation rate when one presentation rate was repeated throughout a trial (i.e., one sound repeated at the same presentation rate in the same trial).

We wanted to replicate these observations with a larger number of pigeons and more complex stimuli than used in the pilot study. Five pigeons, including the three from the pilot study, were tested in a go/no-go same/different procedure that varied rate. Each pigeon received a total of 16 test sessions. The average numbers pecks to the stimulus across time within the trial were measured for this study and for all following experiments. If the birds group each sound presented into an individual object, then changing the presentation rate within the trial would create different objects. This would result in the birds maintaining pecks throughout the trial as the varying rates would cause the same sound to be perceived as more different than same.

Method

Animals

Five male white Carneux pigeons (*Columba livia*; #1N, #2N, #3L, #4T, #5M) were tested throughout all 3 experiments described below. Three pigeons (#1N, #2N, #3L) had been in previously reported auditory experiments (Brooks & Cook, 2010; Cook & Brooks, 2009; Murphy & Cook, 2008). The remaining two birds were added to the experiment later, but received the same initial training as the other three birds (i.e., learning to discriminate series of different pitch, timbre, and complex stimuli from the same repeated stimulus within a trial). All pigeons were tested once daily while being maintained at 85% of their free feeding weight. The

colony was maintained on a 12:12 light:dark cycle with all animals receiving ad libitum water and grit in their home cages.

Apparatus

The operant chamber was a flat-black Plexiglas chamber (42.5 cm wide × 44 cm deep × 39.5 cm high) with an infrared touchscreen (EloTouch) affixed on a 25.5 cm × 21.5 cm window on the front panel of the chamber. This touchscreen was used to record pecks to the auditory stimuli presented via multimedia speakers (HK-195, Harmon-Kardon) located towards the front of the left and right chamber walls. The speakers were positioned behind plastic grills consisting of a 90 cm × 120 cm grid of 5 cm-sized holes. On the top of the box there was a house light which illuminated the box during trials, but was turned off during timeouts. Centrally-located below the touchscreen was a food hopper (Colbourn Instruments) that delivered mixed grain on correct trials. All events within a session were computer-controlled.

Stimuli

Baseline Stimuli. Pigeons had been previously trained to discriminate series of 12 different (S+) stimuli from the same sound repeated 12 times (S-). The stimuli presented during baseline were a mixture of their previously trained stimuli. The stimuli consisted of 12 pitches (six from the third octave and six from the fifth octave), 12 different timbres (e.g., flute, piano, vibraphone, etc.), French horn chords, trumpet chords, and sine waves of each pitch. All these stimuli were truncated to be 1.5 s long with a 50 ms silent inter-stimulus interval (ISI) between sounds in a series resulting in a trial lasting 18.55 s. However, there were also long sounds (e.g., AOL “You’ve got mail” sound) which lasted 2.5 to 4.0 and led to variable length trials. The final

category of stimuli were 72 complex sounds divided into natural sounds (e.g., a cardinal call) and man-made complex (e.g., a door slamming).

All auditory stimuli were previously used as training stimuli and details about how the stimuli were created are available in Cook and Brooks (2009). The pigeons were trained to peck throughout the trial when a series of 12 unique sounds were all presented at the 1.5 s rate, a Different (S+) trial. Similarly, in a Same (S-) trial, the same sound was repeated 12 times at the 1.5 s rate. They were presented to subjects at a loudness of 76-82 dB at the typical pigeon head position within the operant chamber (Radio Shack sound pressure meter; Weighting A). This loudness range had previously been shown to support same-different discriminations in this apparatus (Brooks & Cook, 2010; Cook & Brooks, 2009; Murphy & Cook, 2008). Each test session consisted of 78 baseline trials with all stimuli presented as WAV files.

Test Stimuli. To test how presentation rate affected auditory grouping, all complex stimuli described above were generated at different presentation rates. Presentation rate was manipulated using MATLAB so that each 1.5 s sound (baseline stimulus duration) could be presented at six rates; 0.25 s, 0.50 s, 1.0 s, 1.5 s, (baseline) 2.25 s, and 3.00 s. Using MATLAB, each complex sound was stretched or compressed temporally while maintaining the pitch of the original sound. These rates refer to the duration of each individual sound in the series (e.g., a sound lasting 0.50 s vs. a sound lasting 2.25 s).

Our pilot study showed no effect of the same rate repeating; therefore, we compared two test types (Constant Rate, Varied Rate) for each Sound Condition (Complex, Simple (e.g., pitch stimuli)). The first test type, Constant Rate, presented the same sound at the same rate (e.g., 3.0 s) for the duration of a trial, but a different rate on subsequent Constant Rate trials. The other test

type, Varied Rate, presented the same sound 12 times, but each time at a different rate. The test trials were composed of two presentations of each Sound Condition (Complex man-made, natural; Complex natural sounds; and Simple pitch stimuli), a Constant Rate and a Varied Rate trial type. In the Constant Rate condition, the same sound was presented in a series at the same presentation rate for the entire trial (e.g., Church Bells at 1.5 s, Church Bells at 1.5 s, Church Bells at 1.5 s, etc.). The Varied Rate condition presented the same complex sound throughout the trial, but each time the sound was presented it would be at a different presentation rate (e.g., Church Bells at 0.75 s, Church Bells at 3.0 s, Church Bells at 1.5 s, etc.).

Procedure

All pigeons were previously trained on a go/no-go procedure where they initially pecked a centrally-located 2.5 cm white, circular warning signal. Once pecked, the warning signal would disappear and be replaced by a 6.7 cm purple square where the pigeons directed pecks while auditory stimuli were presented. During a typical trial, a sequence of 12 1.5 s long sounds would be presented with a 50 ms silent inter-stimulus interval (ISI) prior to the next sound in the sequence for a total trial length of 18.5 s. Pecks to the purple square on different trials (S +), go trials, were reinforced on a variable interval schedule of 8.0 s (VI-8) which started when the trial begins. Pigeons received approximately 2.8 s access to mixed grain, except for two older birds (#2N and #3L) who received 6.0 s access. What this means is if they pecked the screen following the variable interval (VI) time elapsing on S+ trials, they would receive mixed grain. Any reinforcement that occurred during a trial did not interrupt the stimulus presentation. Same sequences (S -), no-go trials, were non-reinforced and received a time-out proportional to the number of pecks emitted during the auditory sequence. A small percentage of S+ sequences were non-reinforced and provided an untainted measure of peck rate across the trial without the

influence of cues associated with reinforcement or any missed pecking time as a result of the time spent eating from the hopper. Only the data from probe trials was analyzed in this and following experiments.

The baseline consisted of 78 trials, half S+ (all different series) and half S- (the same sound repeated 12 times in a series), with 10 timbre, 10 pitch, 20 complex sounds (10 natural and 10 man-made), 10 sine waves, 12 long sounds (e.g., AOL “You’ve got mail” sound), 8 French horn chords, and 8 trumpet chords. Six non-reinforced test trials were presented in addition to the baseline trials for a total of 84 trials per session. All trials were randomized within each session and birds received a total of 16 sessions. Within a Varied Rate trial, the same sound was played 12 times, but each of the six rates were played once in the first half of the sound presentations and then repeated in the same order during the second half of the sound presentations. The order of the rates was randomly selected for each trial. The Constant Rate condition was the same as the training Same (S -) condition in which all sounds were presented at 1.5 s. The results from the pilot study indicated that we did not need to test each of the rates in a same condition. Further, each Sound Condition [Complex bird song, Complex man-made sounds, and Simple Pitch sounds] were presented twice per session, once for each Trial Type.

Results

All five pigeons successfully transferred their auditory same-different go/no-go discrimination to stimuli with variable presentation rates. The primary measure used to evaluate their performance was average pecks to the stimulus, either across time or as an aggregated whole. Figure 2 compares the average pecks for the most critical test, varied rate, to the S+ and S- trials across time within the trial. From baseline tests we know that the basic Same/Different discrimination works for both pitch and complex stimuli, but here we see the effects of

presentation rate. Examining only the conditions where the same sound was repeated, but at different rates each time, performance was compared with the baseline same/different conditions. To assess performance, a repeated-measures analysis of variance (ANOVA) was conducted across the five birds on Condition [Complex (collapsed across Sound Type) versus Simple] x Rate Type [Constant Rate versus Varying Rate] x Time in trial. An alpha level of $p < 0.05$ was used as a comparison point to assess statistical significance on all tests. We found a significant main effect of Time In Trial $F(5, 20) = 43.622, p < 0.001$, indicating that responding to the stimuli changed as a function of the time in a trial. There was no significant main effect of Sound Condition, $F(1, 4) = 0.011, p > 0.05$, indicating that across birds there was no difference between Complex and Simple trials. There was also no main effect of Rate Type $F(1, 4) = 0.302, p > 0.05$, indicating that the pigeons responded to the Varied Rate and Constant Rate test trials as same (S -) trials. Finally, there was an interaction between Sound Condition and Time in Trial $F(5, 20) = 3.311, p < 0.05$, indicating that as the number presentations of the stimulus increased the pigeons pecked differently to Complex and Simple sounds.

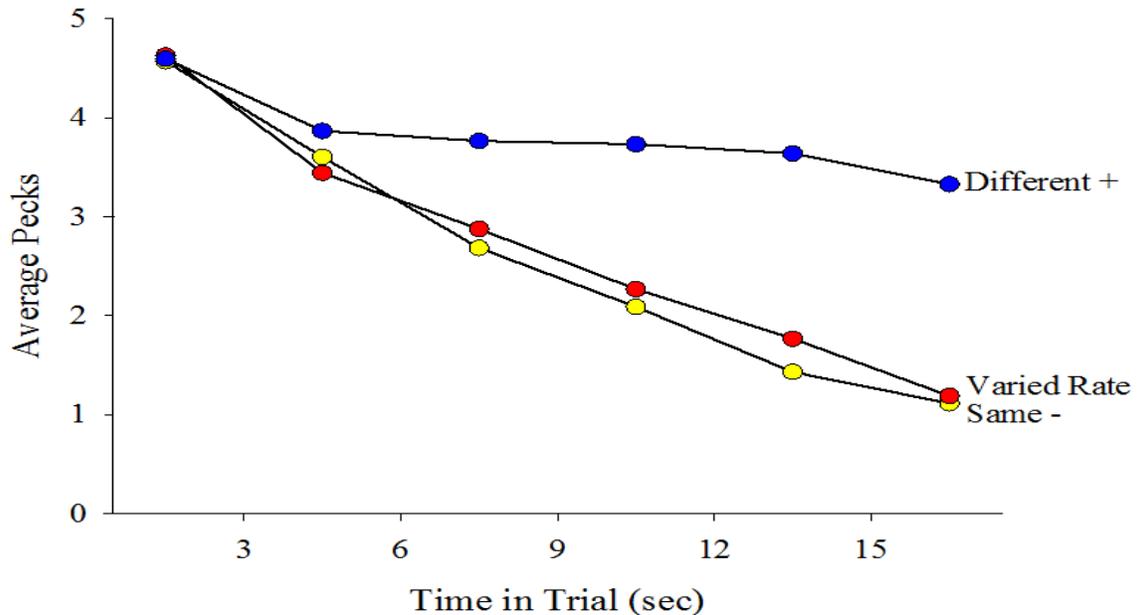


Figure 2. Effect of varying rate on same-different perception. Shows the effect of the test condition compared to the training conditions across time in trial.

Although there was no difference overall, one bird (#1N) appeared to have better discrimination on the complex bird song compared to the simple pitch stimuli so an individual analysis of that bird’s performance across test sessions was conducted. A repeated measures ANOVA across #1N’s 16 sessions of Sound Condition [Natural sound only (a complex stimulus subset) versus Simple pitch stimuli] x Rate Type x Time in Trial revealed a significant main effect of Time in Trial, $F(5, 15) = 338.691, p < 0.001$, which reinforced our previously mentioned finding that discrimination improved as a function of time in the trial. However, when #1N’s man-made complex stimuli were removed from the analysis, a significant interaction effect of Sound Condition and Time in Trial, $F(5, 15) = 9.497, p < 0.05$, was found. This indicated that bird #1N showed an effect of varied rate trials. Additionally, an interaction effect of Sound Condition, Rate Type, and Time in Trial was found, $F(5, 15) = 13.167, p < 0.05$, indicating that the birds perceived natural and pitch stimuli as more different as time progressed in a trial and at faster rates.

Discussion

This experiment demonstrated that a generalist species, the pigeon, on average does not use presentation rate to discriminate auditory stimuli. While one bird did use presentation rate (i.e., pecks to varied rate trials were maintained throughout like a different trial), the remaining four did not use presentation rate to discriminate between sequences. The way they discriminated the Varied Rate condition as an S – trial revealed that the birds were not sensitive to the presentation rate of the stimuli within a trial. That is the varied length of a stimulus did not result

in the stimuli being judge as “different”. Instead it seemed that repetition of the stimuli regardless of duration was the only important factor.

The results of Langer et al. (*in prep*) suggested that presentation rate actually facilitates the formation of auditory objects, but some rates are better than others and that as stimuli become more complex (e.g., repeating a random sequence) the birds lose the ability to discriminate. However, in the current experiment varying rate does not seem to hinder the recognition of “sameness”. Furthermore, other avian species have shown an awareness of rate when it comes to the presentation of territory defense behaviors, such as strophe production length changing as a result of the length of competitor strophe length (Langemann, Tavares, Peake, & McGregor, 2000). However, for auditory stimuli the pigeons do not seem sensitive to rate or duration. It is possible that these stimuli do not present a scenario where this temporal feature was pertinent and that in other situations pigeons would be sensitive to rate.

Experiment 1’s results do not support the hypothesis that the pigeons are forming temporal auditory objects to solve the same-different discrimination based on rate. If the pigeons were forming temporal objects, pecks would be maintained to the Varied Rate trials because the different presentation rates would alter the temporal aspects of the sound. However, the pigeons perceived the Varied Rate trials as more “same” and suppressed their pecks suggesting that presentation rate is not a key feature in how the pigeons complete this discrimination. There are two alternative hypotheses to the object hypothesis that might explain how the birds are solving the go/no-go task. First, the *Gist hypothesis* argues that the pigeons take an average of all the frequencies within a single sound and compare that average frequency to the average frequency of the next sound. Average frequency would not be disrupted by changing the rate a sound was played at; therefore, the pigeons would see a Varied Rate condition as a same stimulus and

suppress their pecks over time, as they did. Second, the *Feature hypothesis* postulates that after considerable experience with this complex stimulus set, the birds have identified key features of each sound. When discriminating within a trial, the birds listen for the key feature of each sound and if the feature is present in both sounds one and two then they respond “same”. Because changing the rate the sounds are played might not completely disrupt these individual features (e.g., unique pitches within the complex sound), the birds respond to the Varied Rate condition as a same trial.

While the presentation rate aided grouping of auditory objects in Langer et al.’s (*in prep*) experiment, it is evident that in the present experiment changing the rate did not change the discrimination. However, the two studies were fundamentally different. Langer et al. (*in prep*) was a between conditions variation of rate while this study was a within condition (in the same trial) variation of rate. It is evident from the current results that if the duration of a sound were a defining feature the birds used to discriminate, they would have seen the Varied Rate trials as different no-go trials. Since the pigeons suppressed their pecks to the Varied Rate condition, it suggests that sound duration is not a feature of their discrimination. So if presentation rate and total sound duration are not utilized, perhaps the sounds’ temporal features used are not based on presentation rate, but more on the stimuli’s internal arrangement.

Experiment 2: Variation in Local Sequence

Experiment 2 sought to examine how the internal, local sequence of a sound affected the pigeons’ auditory discrimination. If the local sequence of a complex sound is used to discriminate that sound from the next sound, as predicted by the Object hypothesis, then reversing that local sequence should disrupt the discrimination. Therefore, if you present the same sound, but alternate playing it forward or reverse (backwards), the pigeons should consider

the same sound forward and reversed as two different sounds. If forward and reversed sounds were treated as equivalent, however, it would be consistent with the Gist and Feature hypotheses.

In the following experiment compared the birds’ peck rates on their training Same (S -) and Different (S +) conditions with two test conditions, Same Reversal and Alternating Reversal. The Same Reversal condition presented a same trial of the reversed sound (e.g., the original sound played backward repeatedly). The Alternating Reversal condition presented the same sound 12 times, but alternated playing the sound forwards or backwards (e.g., forward, reverse, forward, reverse, forward, reverse, etc.). The goal was to see how changing the local sequence, reversing the sound, impacted their established same-different discrimination. Each bird was tested across 12 sessions.

Method

Animals and Apparatus

The same five pigeons and apparatus from Experiment 1 were used.

Stimuli

Experiment 2 used the same training setup and complex stimuli for all test conditions as Experiment 1. However, all the complex stimuli were presented at their original 1.5 s. To test the effect of changing the stimuli’s local sequence, birds’ responses to stimuli played forward were compared to the same stimulus played backwards. The sounds were reversed using a bioacoustical analysis program (SIGNAL 5, Engineering Design, Berkeley, CA). Figure 3 depicts the test condition stimuli with arrows indicating the direction a stimulus is played. For instance, an arrow pointing to the right would mean a sound was played forward while an arrow

pointing to the left would indicate a sound was played backward. Figure 3A depicts an Alternating (S +) trial where two complex sounds, A and B, were alternately repeated but always played forward. Figure 3B depicts an all Same (S -) trial where one complex sound is repeated and always played forward. Finally, Figure 3C depicts the alternating reversal test condition where the trial alternates the forward presentation and reversed presentation of that sound. This AB setup of trials in the all Alternating condition (Figure 3A) was used as a more accurate comparison with the alternating reversal condition (Figure 3C).

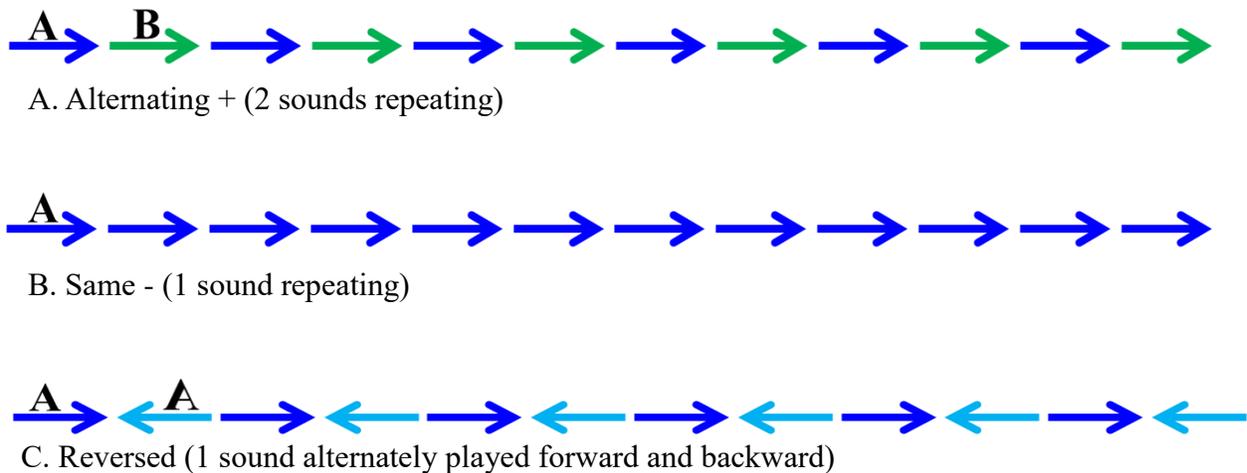


Figure 3. Experiment 2: Local Sequence stimulus conditions. Condition A is composed of two unique sounds played forward in an alternating pattern and represents the training, reinforced, different condition. Condition B is one sound played forward 12 times and is the training same, non-reinforced, stimulus. Condition C is a test condition in which the same sound is presented 12 times, but it is played in an alternating forward, reversed, forward, reversed pattern.

Procedure

Experiment 1’s procedure was also used in Experiment 2. Ten non-reinforced probe trials were presented per session for 12 sessions. Test trials were composed of four Reversed trials (alternating between forward sounds and their reversed counterparts), 2 Alternating (S +) trials

(different trials with only two unique stimuli alternated), 2 training Same (S -) trials, and 2 Reversal Same (the reversed sound played 12 times).

Results

Figure 4 shows the average pecks to conditions, Reversed, Alternating (S +), and Baseline Same (S -), as a function of time in the trial. A repeated measures ANOVA was conducted on Trial Type [Same (S -) versus Reversed] x Time in Trial. Overall, a main effect of Time in Trial, $F(2, 8) = 43.393$, $p < 0.001$, indicating that peck suppression occurred as time progressed in a trial. There was no main effect of Trial Type $F(1, 4) = 4.376$, $p > 0.05$, indicating that the pigeons did not perceive the reversed sounds as different than the forward sounds. Finally, there was no interaction between Trial Type and Time in Trial $F(2, 8) = 0.677$, $p > 0.05$, indicating that even as the birds heard more presentations of the forward/reversed sounds they still did not perceive the sounds as different.

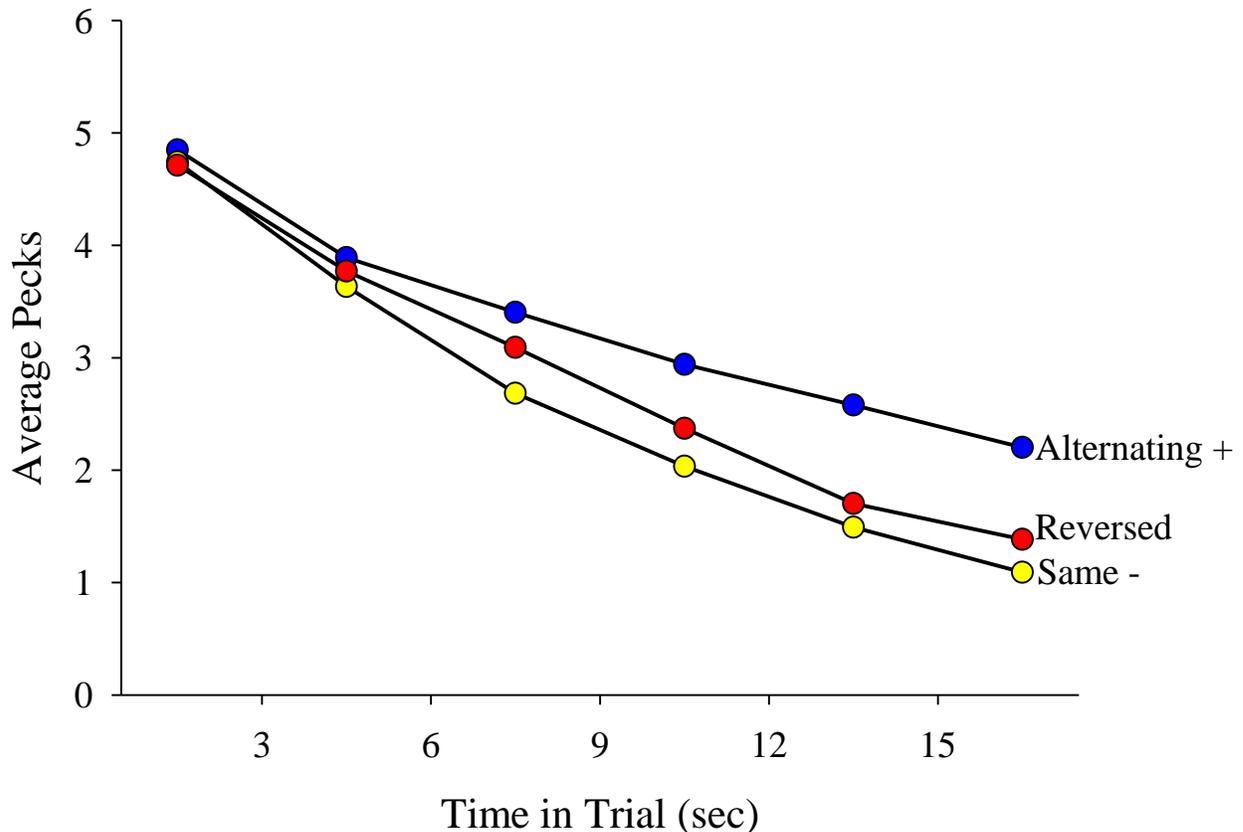


Figure 4. Differences in average pecks to the two control conditions and the test condition in Experiment 2 across time in trial.

Discussion

The results of Experiment 2 reveal that the birds do not use the local sequence of sounds to discriminate between series of stimuli. Songbirds’ reactions to reversed songs has been examined before, but not in this context. Some of those playback studies have found that birds saw reversed and forward stimuli as very different (Goodson & Adkins-Regan, 1997; McCasland & Konishi, 1981). However, Wisniewski and Hulse (1997) demonstrated that like our findings starlings experienced no effect of song order. This suggests a non-auditory learner may perceive auditory stimuli in a similar manner to an auditory expert, the starling.

Unfortunately, these null results do not support the previously presented Object hypothesis, which would suggest that manipulating the local sequence would disrupt the temporal aspects of the auditory object. Just like in Experiment 1, both the Gist hypothesis and the Feature hypothesis can explain how the birds are discriminating between these stimuli. Yet, unique to this experiment was the nature of both the Different condition (Alternating AB) and the main test condition (Alternating Reversal). It could be with fewer number of sounds to compare against the birds saw the Alternating Reversal stimuli as more same than different. Further, changing the AB nature of the stimuli may have produced an effect of the local sequence manipulation.

Experiment 3: Organization Test

Experiment 3 seeks to examine the effect of reorganizing the internal components of each sound while crossing the amount of sound reorganization with entropy. Each complex sound was equally divided into six congruent chunks that will then be reordered as a different temporal

sequence. To ensure that the effect of scrambling was not the sole result of forming smaller objects, we crossed the organization test with entropy. Entropy is a measure of the amount of variability within a categorical variable (Young & Wasserman, 2001) and in this same-different procedure it would be the difference between the number of unique sounds presented per trial. Additionally, pigeons are a neophobic species who would respond less to new or unfamiliar stimuli. By crossing scrambling with entropy, a graded response curve (based on entropy) could be observed and demonstrate whether the cut parts of the sounds (0.25 s) were too small to be perceived.

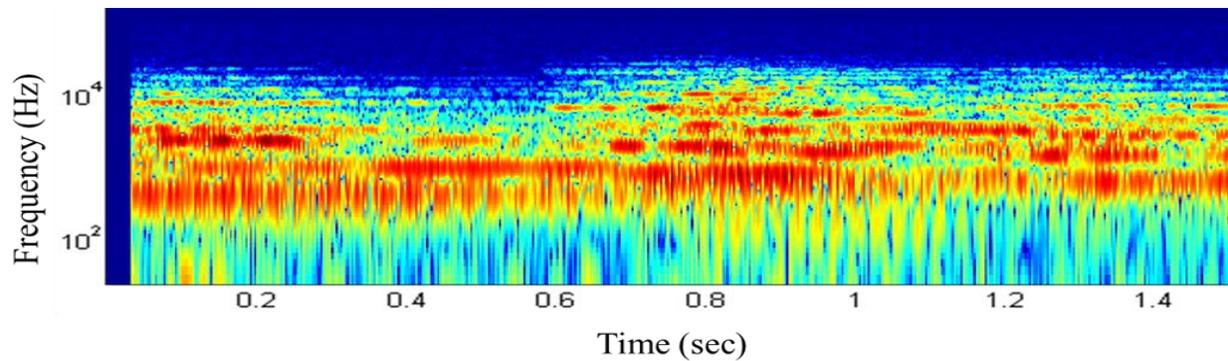
Method

Animals and Apparatus

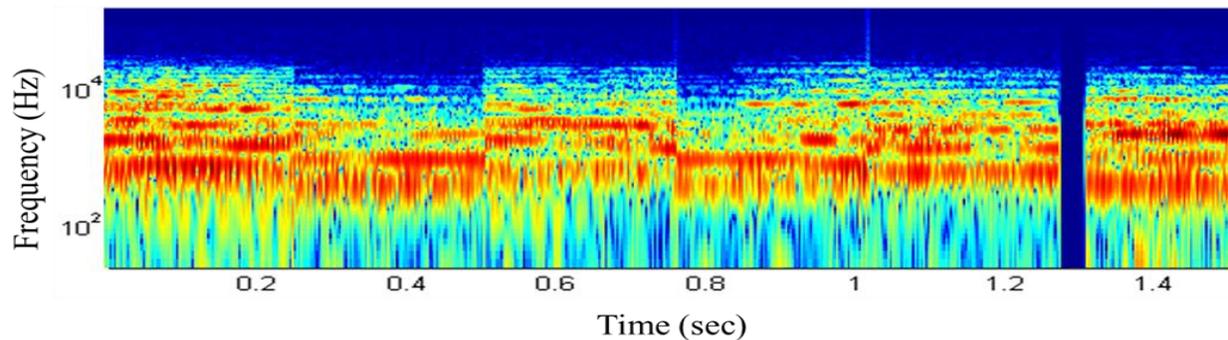
The same five pigeons and apparatus from Experiments 1 and 2 were used here.

Stimuli

The stimuli in this experiment were the same as the previous experiments. In this manipulation, MATLAB was used to take each 1.5 second complex sound and cut it into six equal parts (0.25 s each). The six parts were then scrambled to rearrange the order of the six parts before they were concatenated into a new sound. All possible permutations of the six parts were created and all stimuli were randomly selected so no two birds received the same set of stimuli. A comparison of a training sound spectrogram, canonical (Order = 123456) sound, and one version of a scrambled sound (Order = 423561) can be seen in Figure 5A and Figure 5B, respectively. These two spectrograms depict all the frequencies present at each time slice of the two sounds with brighter colors indicating the amplitude of the waveform.



A. Baseline Sound (Order = 123456)



B. Scrambled Sound (Order = 423561)

Figure 5. Experiment 3: Organization stimulus examples of an unscrambled stimulus (Panel A, Church Bells in canonical order 123456) and scrambled stimulus (Panel B, Church Bells in order 423561). These images are spectrograms depicting the spectral features (e.g., amplitude, power, frequency, etc.) across the duration of the stimulus.

Procedure

Pigeons received 78 training trials and 13 non-reinforced test trials. On any given session, all 13 test trials were only given one complex sound type, either bird song or man-made complex. Additionally, the sounds presented on each trial were controlled across sessions so the sound presented in an S – trial (Same) was the first sound presented in every other test trial. The setup of the test trials was based on Scrambling Type [Training/Baseline, Repeating, Random]. In the Training or Baseline condition, birds were presented S+ and S- trials with the same

canonical order as training. The Repeating Condition selected one sound and a scrambled order (e.g., 412536) and presented it for each presentation of that sound in a trial. Finally, the Random condition presented the same sound repeatedly, but during each presentation there was a different sequence order (e.g., 412536, 162543, 521364, etc.).

The Stimulus Type indicated not only whether the sounds within a trial were scrambled, but also whether the scrambled order of a sound was repeated in a trial. The Training stimuli were presented in the canonical, non-scrambled order as the S – and S + stimuli. The Repeating stimuli were scrambled sounds presented with the same scrambled order every time the sound is played. Therefore, the scrambled order of parts (e.g., 423561) presented the first time a sound was played in a trial would be the same scrambled order every time that sound was presented in that trial. Random trials presented a different scrambled order every time a sound is repeated within a trial.

Results

Figure 6 shows the results of Scrambling Type. A repeated-measures ANOVA was also run on Scrambling Type [Baseline, Repeating, Random] x Time in Trial with the five birds as the repeated measure. No significant main effect of Scrambling Type was found, $F(2, 8) = 0.211, p > 0.05$, indicating that the amount of scrambled items in a series did not change their same responding. A significant main effect of Time in Trial, $F(5, 20) = 11.433, p < 0.001$, was found indicating that pecking to stimuli changed as a function of time in the trial. Finally, there was no significant interaction effect of Scrambling Type and Time in Trial, $F(10,40) = 1.842, p > 0.05$, indicating that even the Time in the Trial did not change the birds’ responding to the amount of

scrambling. Because no differences were found between the Repeating and Random conditions, the two conditions were collapsed into the “Scrambled” data line in the figure.

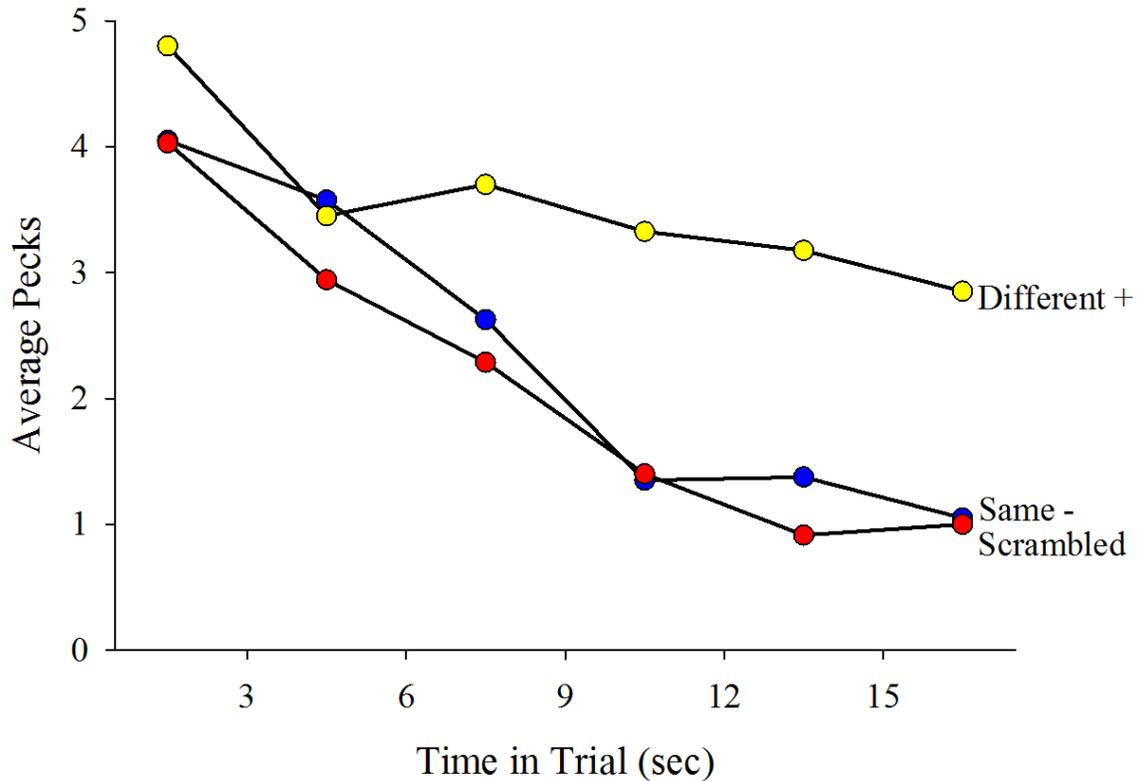


Figure 6. Differences in average pecks to the test condition, Scrambled, compared to the control conditions in Experiment 3 across time in trial.

When the stimuli were scrambled, we inadvertently created acoustic edges that could have introduced variability between the numerous stimulus orders. To determine whether these acoustic edges fundamentally changed the spectral shape compared to the canonical stimulus, we randomly selected a subset of the stimuli to analyze. Using SIGNAL 5 (Engineering Design, Berkeley, CA), a bioacoustical analysis program, we plotted the spectral shape of the canonical sound of Church Bells (Order = 123456) to five randomly selected sound orders. Figure 7

depicts the results of these spectra across the 1.5 s of each sound. We used a smoothing window of 200 Hz with frequency (kHz) on the y-axis and amplitude (dB) on the x-axis. The blue line on each plot depicts the spectral shape of the canonical order for Church Bells while the red line depicts one of the other sequence orders of Church Bells presented to the birds. The main takeaway from these figures is that the spectral shapes of the canonical and non-canonical stimuli are not the same. This implies that the acoustic edges did change the fundamental spectral properties of the scrambled stimuli but did not alter the ability of the pigeons to perceive these sounds as the same.

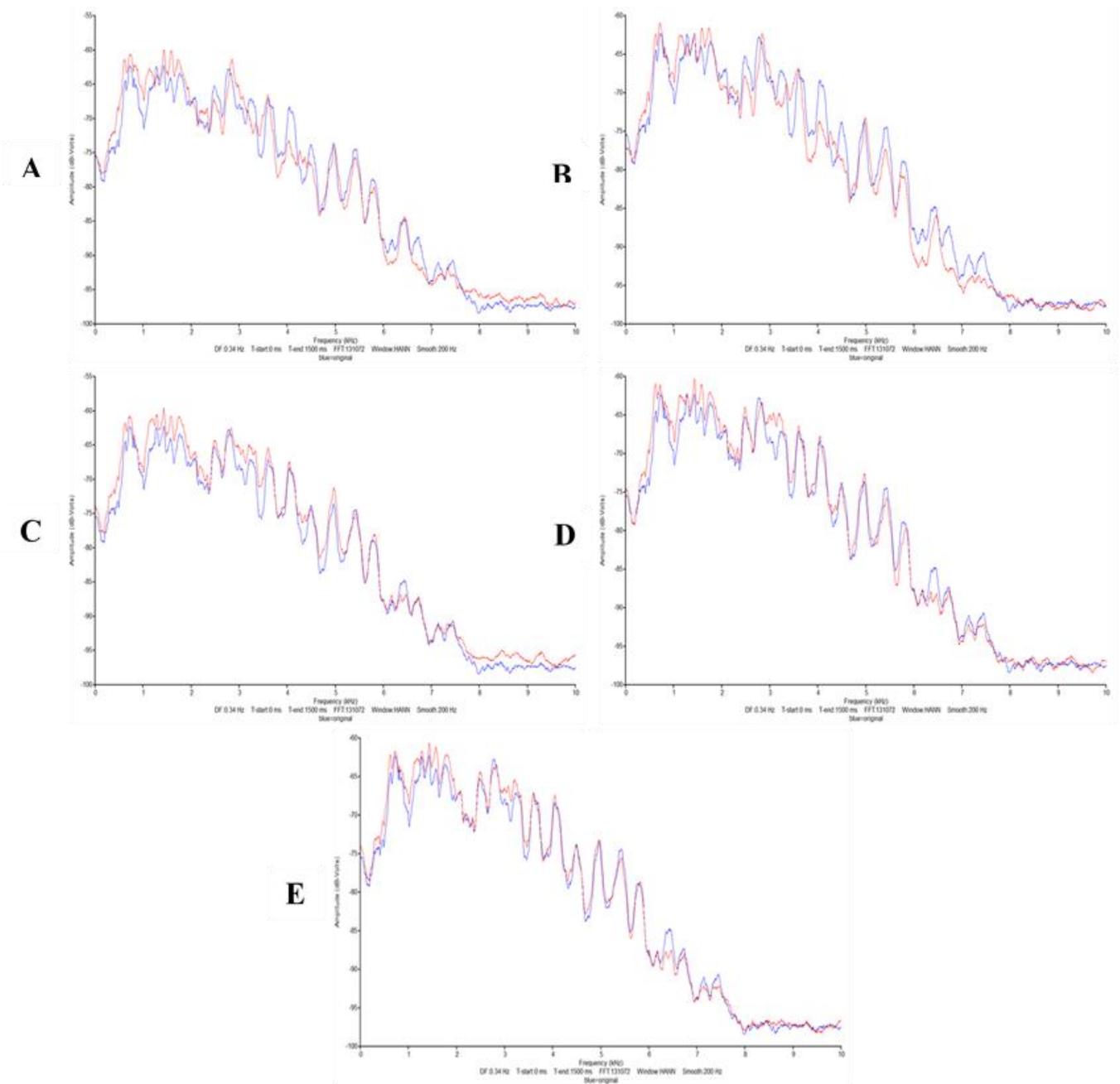


Figure 7. Depicts the spectral shapes of five randomly selected sequence orders of one sound stimulus (Church Bells) compared to the canonical Church Bells stimulus from Experiment 3. Here the spectral shape of the canonical order is presented in blue and each figure compares it to a different sequence order. The sequence order for each panel is as follows: (A) 213654, (B) 315462, (C) 435621, (D) 512463, (E) 614532.

Discussion

Results of Experiment 3 showed no effect of scrambling which implies that temporal organization does not inform this discrimination. Surprisingly, even though scrambling introduced variability in the individual orders of the same sound, the pigeons did not indicate that the sound orders were perceptually different. Experiment 3 also does not conform to the temporal Object Hypothesis as scrambling the individual sounds did not disrupt discrimination of the Scrambled condition in Figure 6 causing responding to be more different. These results are in support of the visual scrambling experiment of Cerella (1980) and of Aust and Huber (2001) who demonstrated that the effects of scrambling may be effected by how familiar a stimulus is to the subject. However, the spectra presented in Figure 7 suggest that the overall spectral shape of the sound was not maintained. This could support a Gist or Feature hypothesis to explain how the pigeons are able to discriminate the various stimulus series.

Similar to Experiments 1 and 2, both the Gist and Feature Hypotheses offer alternative explanations for how the pigeons perceived these scrambled series of sounds. It is possible that the birds’ previous training taught them that organization within a sound was unimportant, so the birds are currently being trained to discriminate between scrambled stimuli. Moreover, 0.25 s sound parts may not have been sufficient to break apart possible features in the auditory stimuli; hence, the pigeons are being trained with sounds with 2, 4, 6, and 8 parts of each sound. Currently, the results suggest there is still no attention being paid to the scrambled organization of these sounds as they maintain their discrimination.

General Discussion

These experiments show that the pigeons’ auditory S/D discrimination is based on time-invariant features. In three separate experiments designed to disrupt their temporal perception of

complex auditory stimuli, the birds consistently indicated that our temporal manipulations did not affect their perception of Same versus Different. Experiment 1 demonstrated that varied presentation rates did not cause a song to be perceived as different. Experiment 2 revealed that songs played backwards were perceived as the same as songs played forward; thus, the pigeons suppressed their pecks to the Reversed trials. Finally, Experiment 3 showed that scrambling parts of an individual song does not result in pigeons perceiving the different scrambling orders as different sounds.

Manipulations of presentation rate, the local sequence, or the organization to a series of the same stimuli did not alter their peck suppression on test trials. These experiments were conducted on the premise that the birds formed auditory objects that were dependent on the temporal features of a single sound compared to the next, the Object Hypothesis; however, this hypothesis was not supported by our data.

These findings are supported by previous research on auditory grouping in vocal learners including starlings (Wisniewski & Hulse, 1997), Zebra finches (Benney & Braaten, 2000), and canaries (Appelants, Genter, Hulse, Balthazart, & Ball, 2005). While these experiments used different methodologies than the one described in this paper, they suggest that vocal learners recognize their own conspecific songs even when other auditory stimuli are present. When presented with distractors, such as the Dawn chorus, some species are better at distinguishing conspecific song from distractors (e.g., Zebra finches) while not as good at distinguishing other species' songs (Benney & Braaten, 2000). Since these species have extensive training with conspecific songs, they can readily identify them despite changes to the total auditory input into the system (i.e., the bird). Benney and Braaten (2000) suggest only biologically-relevant songs can be distinguished which is why Zebra finches cannot distinguish other species' songs from

distractors. However, the pigeons in our study were able to distinguish between various complex stimuli (none of them conspecific sounds) and classify them as a Same or Different series. This suggests the pigeons could learn non-conspecific stimuli and still identify them as the Same despite temporal modifications. These experiments with distractors were not designed as Same/Different discriminations so it is possible that the results would be different if we were using species’ specific stimuli but given the current data we have no support for a temporal feature’s role in the discrimination. Therefore, we revisit the two proposed alternative hypotheses, Gist and Feature, as possible explanations for how the pigeons solved the task.

First, the Gist Hypothesis argues the birds take an average frequency of each sound and compare that average frequency to the average frequency of the next sound. Findings of Experiments 1, 2, and 3 all support this hypothesis to some degree. In Experiment 1, varying the rate of each sound did not interrupt the perception of the Varied Rate condition as same which fits well with this alternative hypothesis. Regardless of the rate each sound was presented at, the average frequency would not change leaving each sound to be perceived as the same. Experiment 2 offered no effect of reversing the sound which is intuitively aligned with this hypothesis as well. Although the local sequence may vary between presentations of a single sound, the overall average frequency would change as a result. Finally, Experiment 3 demonstrated no influence of scrambling the sounds within 0.25 s parts. Even with scrambling the different components, all frequencies within a single sound would be present and average to the same frequency regardless of how much scrambling occurred. While the main findings of each experiment support the Gist Hypothesis, it is not supported by the fact that not all the sounds were suppressed to equally.

Second, the Feature Hypothesis postulates that the birds have identified a key, time-invariant feature of each complex stimulus that they search for. If the feature is present in the first sound and in the second sound, the pigeons perceive the trial as a same trial and suppress their pecking. The results of all three experiments support this hypothesis. First, manipulating the speed a sound is played would not alter or change a feature as the stimuli were carefully constructed to maintain pitch. Second, the reversed sounds still allowed for a label of “same” indicating that the local feature the birds are attending to is time invariant. In the third experiment, the lack of an effect of scrambling may be explained as 0.25 s parts were not fine enough to disrupt the feature; therefore, the feature was not scrambled. Unlike the Gist Hypothesis, the Feature Hypothesis can also explain the variability in peck suppression to different sounds due to the features of some sounds being more salient than those of other sounds.

With the Feature Hypothesis offering the best explanation for how the pigeons are solving the problem, a next step would be to examine this hypothesis in finer detail. One potential experiment would be to programmatically delete parts of each sound to assess whether there are distinct features guiding the auditory discrimination and what those features might be (Kirkpatrick-Steger et al., 1998). This deletion of features will allow us to test for the time invariant feature the birds could be using to discriminate between sounds. After identifying key features of each sound, a follow up to that may be to add the key feature of one sound to another sound and test to see what happens to the discrimination. Furthermore, the types of stimuli presented here are inaccurate in representing what the birds would actually find in their natural environments. In nature, a bird would have to parse the noise, or pertinent auditory information, from the background noise just like starlings did in a study by Wisniewski and Hulse (1997).

Finally, to provide a more complete comparison between humans and pigeons, a next step would be to test humans in a comparable setup using the same auditory stimuli and experimental conditions.

Conclusion

The results of this series of experiments ultimately determined that pigeons do not use time to discriminate between same and different series of stimuli. These findings suggest that there is possibly more than one way to look at auditory grouping which our anthropocentric bias does not allow us to see. Perhaps auditory objects have different features in avian cognition and perception than they do in human cognition and perception. As humans, we take an anthropocentric view of the world and assume that all other organisms must perceive the world in the same way, but the benefits of temporal proximity to our discrimination may not benefit pigeons.

References

- Andersson, S. (1991). Bowers on the savanna: display courts and mate choice in a lekking widowbird. *Behavioral Ecology*, *2*, 210-218.
- Appeltants, D., Gentner, T. Q., Hulse, S. H., Balthazart, J., & Ball, G. F. (2005). The effect of auditory distractors on song discrimination in male canaries (*Serinus canaria*). *Behavioural processes*, *69*(3), 331-341.
- Aust, U., & Huber, L. (2001). The role of item- and category-specific information in the discrimination of people- versus nonpeople images by pigeons. *Animal Learning & Behavior*, *29*(2), 107-119. doi: 10.3758/Bf03192820
- Aust, U., & Huber, L. (2003). Elemental versus configural perception in a people-present/people-absent discrimination task by pigeons. *Learning & Behavior*, *31*(3), 213-224. doi: 10.3758/BF03195984
- Benney, K. S., & Braaten, R. F. (2000). Auditory scene analysis in Estrildid finches (*Taeniopygia guttata* and *Striata domestica*): A species advantage for detection of conspecific song. *Journal of Comparative Psychology*, *114*(2), 174.
- Bregman, A. S. (1994). *Auditory scene analysis: The perceptual organization of sound*. Cambridge, MA: The MIT Press.
- Bregman, A. S., & Campbell, J. (1971). Primary auditory stream segregation and perception of order in rapid sequences of tones. *Journal of Experimental Psychology*, *89*(2), 244.
- Brooks, D. I., & Cook, R. G. (2010). Chord Discrimination by Pigeons. *Music perception*, *27*(3), 183-196. doi: 10.1525/mp.2010.27.3.183
- Cerella, J. (1980). The pigeon's analysis of pictures. *Pattern recognition*, *9*, 1-6. doi: 10.1016/0031-3203(80)90048-5

- 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. doi: 10.1037/a0012621
- Cook, R. G., Qadri, M. A. J., & Keller, A. M. (2015). The analysis of visual cognition in birds: Implications for evolution, mechanism, and representation. *Psychology of Learning and Motivation*, *63*, 173-210. doi: 10.1016/bs.plm.2015.03.002
- Farr, J. A. (1980). Social behavior patterns as determinants of reproductive success in the guppy, *Poecilia reticulata* Peters (Pisces: Poeciliidae). *Behaviour*, *74*(1/2), 38-91.
- Gibson, R. M., & Bradbury, J. W. (1985). Sexual selection in lekking sage grouse: Phenotypic correlates of male mating success. *Behavior Ecology and Sociobiology*, *18*, 117-123.
- Goodson, J. L., & Adkins-Regan, E. (1997). Playback of crows of male Japanese quail elicits female phonotaxis. *Condor*, *99*(4), 990.
- Hulse, S. H., MacDougall-Shackleton, S. A., & Wisniewski, A. B. (1997). Auditory scene analysis by songbirds: Stream segregation of birdsong by European starlings (*Sturnus vulgaris*). *Journal of Comparative Psychology*, *111*(1), 3.
- Kirkpatrick-Steger, K., Wasserman, E. A., & Biederman, I. (1998). Effects of geon deletion, scrambling, and movement on picture recognition in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, *24*(1), 34-46. doi: 10.1037/0097-7403.24.1.34
- Kirkpatrick, K. (2001). Object perception. In R. G. Cook (Ed.), *Avian visual cognition*. [Online].
- Langemann, U., Tavares, J. P., Peake, T. M., & McGregor, P. K. (2000). Response of great tits to escalating patterns of playback. *Behaviour*, *137*(4), 451-471.

- Langer, M. S., Qadri, M. A. J., Keller, A. M., & Cook, R. G. (*in prep*). Auditory object formation in pigeons and humans.
- Magnus, D. B. E. (1958). Experimental analysis of some "overoptimal" sign-stimuli in the mating behaviour of the fritillary butterfly *Argynnis paphia* L. (Lepidoptera: Nymphalidae). *Proceedings of the Tenth International Congress of Entomology*, 2, 405-418.
- McCasland, J., & Konishi, M. (1981). Interaction between auditory and motor activities in an avian song control nucleus. *Proceedings of the National Academy of Sciences*, 78(12), 7815-7819.
- 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. doi: 10.1016/j.beproc.2007.10.008
- Rowland, W. (1995). Do female stickleback care about male courtship vigour? Manipulation of display tempo using video playback. *Behaviour*, 132(13), 951-961.
- Tougas, Y., & Bregman, A. S. (1985). Crossing of auditory stimuli. *Journal of Experimental Psychology*, 11(6), 788-798.
- Tougas, Y., & Bregman, A. S. (1990). Auditory streaming and the continuity illusion *Perception and Psychophysics*, 47, 121-126.
- Wagemans, J., Elder, J. H., Kubovy, M., Palmer, S. E., Peterson, M. A., Singh, M., & van der Heydt, R. (2012). A century of Gestalt psychology in visual perception I. Perceptual grouping and figure-ground organization. *Psychological Bulletin*, 138(6), 1172-1217.
- Wisniewski, A. B., & Hulse, S. H. (1997). Auditory scene analysis in European Starlings (*Sturnus vulgaris*): discrimination of song segments, their segregation from multiple and

reversed conspecific songs, and evidence for conspecific song categorization. *Journal of Comparative Psychology*, 111(4), 337.

Young, M. E., & Wasserman, E. A. (2001). Stimulus control in complex arrays. In R. G. Cook (Ed.), *Avian Visual Cognition*: <http://www.pigeon.psy.tufts.edu/avc/young/>.