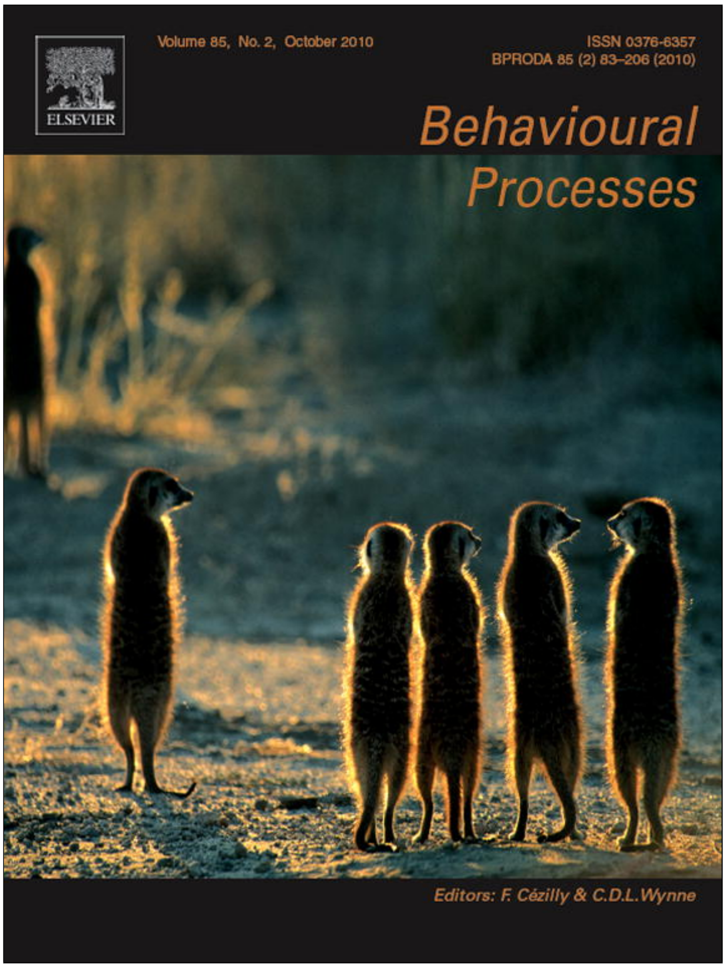
Volume 85, No. 2, October 2010
ISSN 0376-6357
BPRODA 85 (2) 83–206 (2010)
ELSEVIER
Behavioural
Processes
Editors: F. Cézilly & C.D.L.Wynne

Behavioural Processes 85 (2010) 99–110

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Testing meter, rhythm, and tempo discriminations in pigeons

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ARTICLE INFO

Article history:
Received 3 May 2010
Received in revised form 22 June 2010
Accepted 22 June 2010

Keywords:
Pigeons
Auditory discrimination
Rhythm
Tempo
Music

ABSTRACT

Rhythmic grouping and discrimination is fundamental to music. When compared to the perception of pitch, rhythmic abilities in animals have received scant attention until recently. In this experiment, four pigeons were tested with three types of auditory rhythmic discriminations to investigate their processing of this aspect of sound and music. Two experiments examined a meter discrimination in which successively presented idiophonic sounds were repeated in meters of different lengths in a go/no-go discrimination task. With difficulty, the birds eventually learned to discriminate between 8/4 and 3/4 meters constructed from cymbal and tom drum sounds at 180 beats per minute. This discrimination subsequently transferred to faster tempos, but not to different drum sounds or their combination. Experiment 3 tested rhythmic and arrhythmic patterns of sounds. After 40 sessions of training, these same pigeons showed no discrimination. Experiment 4 tested repetitions of a piano sound at fast and slow tempos. This discrimination was readily learned and showed transfer to novel tempos. The pattern of results suggests that pigeons can time periodic auditory events, but their capacity to understand generalized rhythmic groupings appears limited.

1. Testing meter, rhythm, and tempo discriminations in pigeons

The production and appreciation of music is virtually a defining characteristic of our species. Because of this, interest in understanding the evolution and function of music and its constituent components has recently increased (Hauser and McDermott, 2003; McDermott and Hauser, 2005; Patel, 2008; Wallin et al., 2000). Correspondingly, the comparative examination of music has grown in an attempt to help address such issues. For instance, there are several demonstrations that various human music genres or styles can be discriminated by animals (Chase, 2001; Porter and Neuringer, 1984; Watanabe and Nemoto, 1998; Watanabe and Sato, 1999). Because of music's tonal and rhythmic complexity, however, such demonstrations reveal little about how animals process the fundamental melodic, harmonic, and rhythmic components of music.

The processing of pitch has received the most attention in animals (Brooks and Cook, 2010; D'Amato and Colombo, 1988; Watanabe and Sato, 1999; Wright et al., 2000), while far less attention has been devoted to their perception and production of rhythm (Hulse et al., 1992; McDermott and Hauser, 2005). This is surprising because drumming, and correspondingly dance and movement, were likely the earliest forms of hominid music production and appreciation. In early hominids, concurrent drumming and dancing likely functioned to promote group cohesion (Kirschner and Tomasello, 2009) and synchronous activity in the brain is known to be reinforcing (McFadden, 2002; Penhune et al., 1998). It may have also served a communicative function similar to tree drumming behavior in chimpanzees and macaques (Boesch, 1991; Remedios et al., 2009). Head bobbing and foot drumming are also effective means of signal transmission for lizards and rodents (e.g., Macedonia et al., 1994; Randall, 2001). Even in early life musical rhythm is appreciated, as human infants more easily detect tonal changes in auditory sequences that have a strong metric framework (Bergeson and Trehub, 2006).

Rhythm is created from repeated occurrences of multiple idiophonic beats or utterances. Patel (2008) defines rhythm as the "systematic patterning of sound in terms of timing, accent, and grouping" (p. 96). When accented and unaccented sequences of repeated sounds are presented, a meter can be established that enables the grouping of the beats into measures. For example, a waltz meter in 3/4 time consists of repeated measures of three quarter note beats. The first beat of each measure is typically accented, by either loudness or timbre, to clarify the grouping of these beats. Variables such as tempo and syncopation, which alter the timing between the beats, also aid rhythmic grouping (Fitch and Rosenfeld, 2007). Tempo increases when beats occur more frequently in time. Syncopation increases when some beat onsets are inconsistent with an established pulse. Such inconsistent beats are referred to as off-beats, and their usage shows that rhythmic grouping does not require isochronous sequences of events. Instead it is the predictability of events and the expectancies created by them that are most important in creating affective states in humans (Huron, 2006).

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doi:10.1016/j.beproc.2010.06.015

Hulse et al. (1984) found that starlings (*Sturnus vulgaris*) could readily discriminate rhythmic and arrhythmic patterns of repeated tone sequences and transfer this discrimination to novel tempos. Hulse and Kline (1993) taught starlings to discriminate brief tones varying in tempo (4 and 8 or 8 and 16 pulses per sec) in a two-alternative choice task. This learning later transferred to two new tempos when the assignment of the "fast" and "slow" keys remained the same between tasks. McDermott and Hauser (2007) found that cotton-top tamarins (*Saguinus oedipus*) and marmosets (*Callithrix jacchus*) prefer repeated clicks played at slower tempos (60 bpm) than faster ones (400 bpm), although they also showed a general preference for silence over music. Harley et al. (2002) showed that dolphins (*Tursiops truncatis*) can discriminate up to six different 4-s rhythms by performing different behaviors to each rhythm on cue.

Attention to rhythm perception in animals has recently been sharpened because of its potential theoretical and evolutionary connections to vocal learning. Because vocal learning and the synchronization of movement to a rhythmic beat both involve tight auditory-motor integration, Patel has recently theorized that vocal learning is the neurobiological foundation for rhythmic motor synchronization to music (Patel, 2006, 2008). Notably, both behaviors seem to rely on some common brain regions, such as the basal ganglia (Feenders et al., 2008; Patel, 2006). The similar expression of genes, such as FoxP2, has been observed in basal ganglia circuits of both songbirds and humans during vocalization learning (Peretz, 2009; Teramitsu et al., 2004). As a result, considerable interest has focused on whether beat perception and synchronization (BPS) – the ability to move in time with a musical beat – occurs in animals. Patel's (2006) "vocal learning and rhythmic synchronization hypothesis" predicts that only vocal-learning species are capable of entraining rhythmic movements to a beat. Under this hypothesis, for example, chimpanzees and bonobos (vocal non-learners) would not be expected to synchronize their movements to rhythmic beats, despite the fact that they can produce regular rhythmic actions (Kugler and Savage-Rumbaugh, 2002). Some evidence supportive of Patel's hypothesis is the ability of "Snowball," the dancing sulphur-crested cockatoo (*Cacatua galerita)* to synchronize to the beat of human music across different tempos (Patel et al., 2009). Additionally, Patel and Iversen (2006) found that an Asian elephant could maintain a slow but periodic beat on a drum with less variation than found in humans consistent with recent research that points to vocal learning and imitation in elephants (Poole et al., 2005). Videos of elephants have also been analyzed to show movement in synchrony to music, as well as in several other vocal learning species (Schachner et al., 2009). Because of the theoretical implications of the vocal learning hypothesis, it has become increasingly criticial to examine rhythmic perception and production in animals, especially as related to whether they learn their vocalizations or not.

In the current experiment, we investigated the perception of rhythm in pigeons using different types of discriminations involving repeated auditory stimuli. Because they are non-songbirds with an unlearned vocabulary of about five vocalizations for social interactions (Baptista and Abs, 1983), pigeons are an interesting species to test in this context. Our prior research has established that pigeons can process same/different sequences of different types of auditory stimuli (Cook and Brooks, 2009; Murphy and Cook, 2008). Brooks and Cook (2010) found that their processing of harmonically complex chord stimuli shares similarities with that of humans. An evaluation of their capabilities to perceive rhythmic structures should advance our understanding of Patel's vocal learning hypothesis, the columbiform auditory system more generally, their cognitive processing of sequential and temporal information, and the comparative distribution of the precursors and mechanisms of potentially musical capabilities.

In four experiments we tested pigeons with three forms of rhythmic discriminations. Experiments 1 and 2 tested four pigeons with a meter discrimination, in which the birds had to discriminate between groupings of different percussive sounds that varied in number of beats per measure. In Experiment 3 they were tested with a discrimination between sequences with rhythmic (isochronous) and arrhythmic (non-isochronous) patterned intervals. Finally, Experiment 4 tested them in a tempo discrimination in which a single sound was repeated at a fast or slow rate.

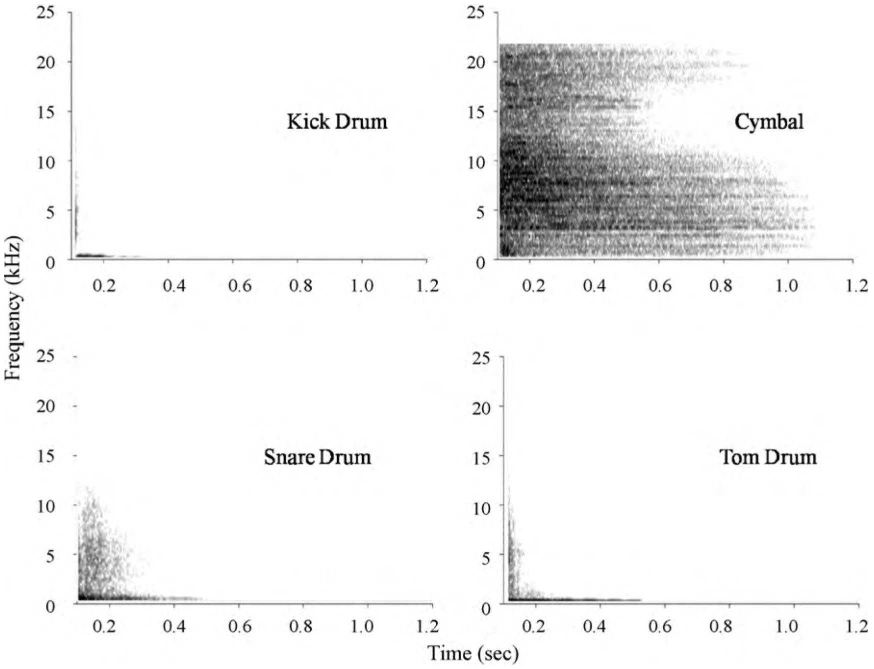

Fig. 1. Spectrograms of the four percussive sounds tested in Experiments 1–3.

2. Experiment 1 – meter discrimination

Experiment 1 tested pigeons on their capacity to process different meters. Meters are rhythmic patterns that derive from the series of strong accented and weak unaccented beats relative to the main pulse of a rhythm. These accents can come in the form of differences in loudness or timbre and are critical to the cognitive organization of music in humans (Clarke, 1987; Keller and Repp, 2005; Parncutt, 1994). Duple (4/4 or common time) and triple (3/4 or waltz time) meters are common examples in music. This important aspect of rhythm has not been well explored in animals. To our knowledge, this is the first attempt to examine this issue.

The experiment had several phases. Because we wanted to establish a generalized meter discrimination, we first attempted to train the pigeons with three different meters at two different tempos. Meter is invariant over changes in tempo because of their constant relation between the number of accented and unaccented beats. To create the accented and unaccented beats we used two different idiophonic timbres: kick (K) and snare (S) drum sounds (see Fig. 1 for spectrograms of each sound tested in Experiment 1). We used these sounds because of their steep attack times and spectral distribution. Research with pigeons has suggested they can time artificial and naturalistic stimuli equally well (Miki and Santi, 2001). This first phase of the experiment tested 3/4, 4/4, and 5/4 meters against each other. The 4/4 meter (KS4+) was designated the S+ condition and the other two meters served as the S− conditions (KS3−, KS5−) in a go/no-go discrimination procedure. The continually repeating measures consisted of a kick drum on the first beat followed by the snare drum on all remaining beats in a measure (e.g., KS3− = KSS; KS4+ = KSSS; KS5− = KSSSS). These contrasting meters were presented at 100 and 120 bpm (beats per minute) over trials. We tested these three meters with little success over the initial 25 sessions.

In Phase 2, we simplified the discrimination by testing only KS3− and KS4+ conditions at a single tempo (120 bpm). With no evidence of learning with this change, in Phase 3 we increased the tempos to 140, 160, and 180 bpm to better promote the grouping of the different beats. Phase 4 continued this strategy by just testing the fastest tempo for an additional 45 sessions.

Because of the pigeons' continued learning difficulties, we decided to change the drum sounds for the different beats. From this point on, a cymbal (C) and tom drum (T) sounds were used to create each meter. The 30 sessions of Phase 5 (CT4+ vs. CT3− 180 bpm) with these new sounds still resulted in no discrimination learning. Finally in Phase 6, we increased the discriminability of the meter by changing the S+ condition to 8/4 time. Thus, the sequences now consisted of a cymbal on the first beat followed by the tom on the following two or seven beats until the pattern repeated (CT8+ = CTTTTTTT vs. CT3− = CTT). With this new organization presented at 180 bpm, the pigeons began to learn the discrimination. After the discrimination stabilized, we conducted a series of tests presenting just the first beat or the other beats of each measure to investigate the basis for this auditory discrimination.

3. Method

3.1. Animals

Four experimentally naïve male White Carneaux pigeons (*Columba livia*; obtained from Palmetto Pigeon Plant, Sumter, SC) were tested. The birds were maintained at 80–85% of their free-feeding weight during testing with free access to water and grit. They were housed in a colony room with a 12:12-h light–dark cycle.

3.2. Apparatus

Testing was conducted in a flat black Plexiglas-paneled operant chamber (15.5″ wide × 16.5″ high × 14″ deep) contained within a sound-dampening chamber made of homasote soundboard lined with 1″ layer of soundproofing foam (Super Soundproofing Co.; San Marcos, CA). Visual stimuli were presented on a 17″ LCD computer screen (NEC Inc.; Tokyo, Japan) behind a 17″ infrared touchscreen (EloTouch Inc.; Harrisburg, PA) which detected and recorded pecks. The auditory stimuli were simultaneously presented from two speakers (Boston Acoustic CR57; Peabody, MA) driven by a stereo receiver (Sherwood RX4105; Cerritos, CA) that received its input from the computer's sound card (SoundMAX Integrated Digital Audio, Analog Devices, Inc.; Taipei, Taiwan). The speakers were played through 24 × 16 cm perforated metal grills at the front of either side of the chamber. A houselight in the chamber's ceiling was illuminated at all times, except timeouts. A centrally located food hopper below the touchscreen delivered mixed grain.

Auditory stimuli were software-generated synthesized waveforms composed with the Rhythm Rascal loop generator (rhythmrascal.com). These were recorded as 16-bit WAV files sampled at 44.1 kHz. The training stimuli were made from four percussion sounds from the software's default library: kick drum (K), snare drum (S), cymbal (C), and tom drum (T). These sounds were distinct to human ears and within the known auditory frequency range of the pigeons (Goerdel-Leich and Schwartzkopff, 1984; Heise, 1953). These sounds were presented at 75–85 db as measured from the pigeon's typical position in the chamber (Radio Shack sound pressure meter; Weighting A).

3.3. Procedure

3.3.1. Go/No-Go trials

Discrimination training started following hopper and autoshaping training. Pigeons were tested using a go/no-go procedure. Each trial started with a peck to a centrally located 2.5 cm circular white ready signal. This was then replaced by a 6.7 cm purple square, to which the birds directed pecks during sound presentations. Sound presentations were 28 s in duration. The pigeons had to discriminate between meters with different numbers of repeating isochronous beats. Pecks during S+ trials were reinforced with 2-s access to grain on a variable interval (VI-10) schedule. During reinforcement, the sounds continued to play. They were also given 2-s response-independent access to grain following the end of each S+ trial. A small percentage of randomly selected S+ trials were conducted as non-reinforced probe trials in each session. This was done to obtain peck rate data uncontaminated by the presence of reinforcement and feeding behavior within a trial. Pecks during S− trials were not reinforced and also resulted in a 1-s per peck dark timeout after the termination of the sound (maximum = 120 s). An ITI of 5 s separated each trial.

3.3.2. Phase 1

Initial training involved repeating measures that consisted of three, four, or five beats at tempos of 100 and 120 bpm. Each of these three meters used a kick drum as the first beat of each measure followed by the snare drum on the subsequent beats of each measure (KS3− = KSS; KS4+ = KSSS; KS5− = KSSSS). All beats were isochronous, with each sound starting every .6 s (100 bpm) or .5 s (120 bpm) depending on tempo. Within one tempo, the duration of each measure thus depended on the meter (100 bpm: KS3− = 1.8 s; KS4+ = 2.4 s; KS5− = 3 s; 120 bpm: KS3− = 1.5; KS4+ = 2 s; KS5− = 2.5 s). Each session consisted of 72 randomly ordered trials (24 KS4+/24 KS3− and 24 KS5− trials) with half of these trials conducted at each tempo. Two positive KS4+ trials for each tempo were randomly selected to be probe trials in each session. Twenty-five sessions using this organization were conducted.

3.3.3. *Phase 2*

Because the pigeons exhibited no learning, we simplified the task by removing trials testing the KS5− meter and the 100 bpm tempo. Each session now consisted of 72 randomly ordered trials (36 KS4+/36 KS3−) tested at the 120 bpm tempo. Four probe trials were tested in each session. Ten sessions using this organization were conducted.

3.3.4. *Phase 3*

To increase the possibility of grouping, in Phase 3 we increased the tempos of the different meters to 140, 160, and 180 bpm. Each session consisted of 96 randomly ordered trials (48 KS4+/48 KS3−) with each tempo being tested equally often with each meter. Two probe trials per tempo were tested for each session. Thirty sessions using this organization were conducted.

3.3.5. *Phase 4*

Because the pigeons still exhibited no learning, we simplified the task by testing only the fastest 180 bpm tempo. Each session consisted of 96 randomly ordered trials (48 KS4+/48 KS3−). Two probe trials were tested each session. Forty-five sessions using this organization were conducted.

3.3.6. *Phase 5*

Because the kick and snare sound might somehow be poor stimuli for the pigeons, we introduced and tested the cymbal and tom sound. The cymbal was used as the first beat for each type of meter (CT4+ = CTTT; CT3− = CTT). The organization of these sessions was otherwise the same as in Phase 4. Each session consisted of 96 randomly ordered trials (48 CT4+/48 CT3−) tested at the 180 bpm tempo. Two probe trials were tested each session. Thirty sessions using this organization were conducted.

3.3.7. *Phase 6*

These new stimuli resulted in no immediately better performance, so we increased the difference between the two meters. Thus, the CT4+ condition was changed to CT8+ (CTTTTTTT). Each session now consisted of 96 randomly ordered trials (48 CT8+/48 CT3−) tested at the 180 bpm tempo. Two probe trials were tested each session. Fifteen sessions using this organization were conducted. At this point, to shorten the length of the sessions and keep the pigeons' within their weight range, we shortened the duration of trial presentations from 28 to 20 s, stopped reinforcing at the end of S+ trials, and increased the number of probes to four per session. Including the test sessions described in the next section, 55 sessions were conducted using the new CT8+ meter.

3.3.8. *Single stimulus tests*

After 20 sessions of Phase 6, we tested the pigeons with probes that presented only a single sound from each type of meter. *Beat 1 tests* presented only the sound used for the first beat, followed by silence in place of the remaining beats in each measure (Cx). *Other beat tests* presented the sounds used for the remaining beats of each measure, preceded by silence in place of the first beat (xT). For each session, four beat 1 probe trials (2 Cx8/2 Cx3) and four other beat probe trials (2 xT8/2 xT3) were randomly intermixed within the 96-trial organization described for Phase 6. Eight sessions of this testing were conducted.

3.4. *Results*

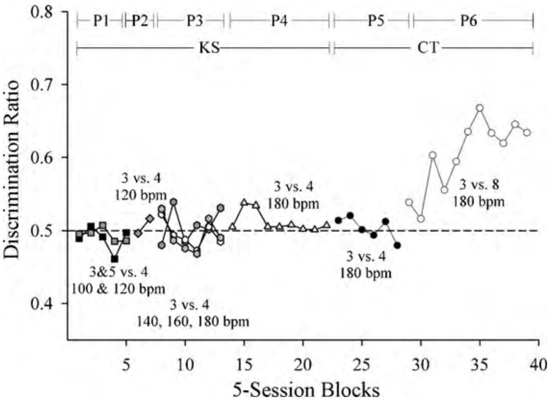

Fig. 2. Mean discrimination ratios in 5-session blocks for the six different phases (different shaped symbols) of Experiment 1. The labels at the top indicate the phase number and labels below that indicate which stimulus sets were used in each phase. The dotted line indicates chance performance.

Overall, the pigeons did not learn the meter discrimination until we increased the discriminability in Phase 6. Fig. 2 shows mean discrimination ratio (DR = S+ pecks/[S+ pecks + S− pecks]) across the six phases of Experiment 1. These and all subsequent calculations of S+ peck rates were derived from the non-reinforced probe trials. Over the first four phases using different organizations of the KS stimuli, there was no evidence of learning after 110 sessions of training. The average DR (M = .49) for all four pigeons during Phase 1 was not different from chance (.50). The subsequent phases in which we modified the tempo of the different meters resulted in no better performance (Phase 2, M = .51; Phase 3, M = .50; Phase 4, M = .51). A series of one way repeated measures ANOVAs examining DR across 5-session Blocks of each phase yielded no evidence of learning in any phase, as the main effect of Blocks was not significant in any of these analyses (all statistical tests in this paper were evaluated using an alpha level of .05 or less). The introduction of the CT stimuli in Phase 5 also did not immediately produce discrimination over the 30 sessions of testing 4/4 and 3/4 meters (mean DR = .50). A repeated measures ANOVA of DR over the six 5-session Blocks revealed no significant effect of block, $F(5,15) = 0.47$. Thus, despite several modifications in tempo and timbre across these five phases, the pigeons' mean performance at discriminating 4/4 and 3/4 meters across all phases was at chance.

With the introduction of a greater difference between the meters in Phase 6, the pigeons acquired the discrimination. This acquisition can be seen in the rightmost portion of Fig. 2. A repeated measures ANOVA of DR over 5-session Blocks confirmed this increase in discrimination, $F(10,30) = 4.1$. As determined from the last 15 of the 55 training sessions, all four birds collectively, $t(3) = 3.6$ and individually, all $ts(14) > 1.76$, differentiated among the two meters at above chance levels.

We next examined how quickly the birds accumulated this information over time within a trial. The earliest possible point of discrimination among the two meters occurred after hearing the fourth beat. Thus, if the fourth beat was different from the previous beat and the same as the first beat, the trial was in 3/4 meter. If the sounds of the third and fourth beats were the same, the trial was in the 8/4 meter. Given a 180 bpm tempo, this happened one second into the trial. To examine the time course of the pigeons' detection of the two meters within a trial the following analysis was conducted. Pecks across a trial were divided into 2-s bins. Pecks for each individual pigeon were then normalized relative to that bird's maximum peck rate across these bins. The results of this analysis are shown in Fig. 3. It shows the time course of S+ and S− responding within a trial for the first 15 (top panel) and last 15 (bottom panel) sessions of Phase 6. The pigeons started each trial by pecking the display with discriminative behavior emerging over time as evidenced by the higher maintained peck rates during the CT8+

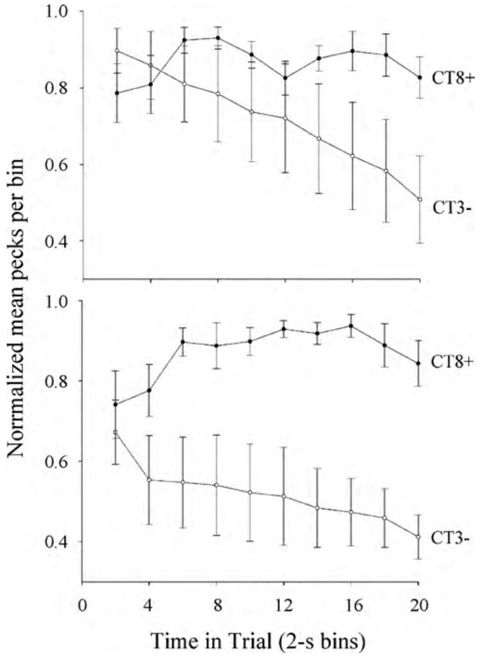

Fig. 3. Mean normalized pecks for all birds across time within an auditory presentation during the first (top panel) and last 15 (bottom panel) sessions of Phase 6. Error bars show the SEM.

condition and the monotonically declining peck rates in the CT3− condition.

During the early sessions, discriminative behavior emerged later in the trial than during the later sessions of training after discrimination had improved. To quantify how quickly the birds discriminated within a trial, we used a series of paired t-tests to compare the mean peck rates across the 2-s bins for the CT8+ vs. CT3− conditions. This was done separately for each bird. During the first 15 sessions, these comparisons revealed that peck rates significantly diverged for all birds by the end of the trial. Bird #1B performed best, discriminating the two conditions by the sixth second. Bird #2C discriminated by the 22nd, #3J by the 20th, and #4L by the 26th second. With further training, the speed of making this sequential discrimination improved for all birds. Over the last 15 sessions of training, three of the birds now showed significant differences in peck rates by the fourth second, with the worst performing bird, #4L, doing so by the 16th second.

3.4.1. Single stimulus tests

The pigeons transferred best (mean DR = .61) to stimuli with the cymbal sound on the first beat followed by silence in each measure (Cx). Performance was only slightly better than chance (mean DR = .53) when there was a rest on the first beat followed by tom beats (xT). The birds pecked significantly more often, $t(3) = 3.06$, on Cx8 tests ($M = 17.7$) than the Cx3 tests ($M = 11.4$). This difference was not significant on the xT8 ($M = 19.5$) and xT3 ($M = 17.1$) tests, $t(3) = 1.3$.

3.5. Discussion

Overall, these meter discriminations proved difficult for the pigeons to learn. The pigeons never successfully learned to discriminate 3/4 from 4/4 meter over the course of 12,600 trials during which we changed tempos, stimuli, and number of beats per measure. Only with the eventual introduction of the sharply contrasting 8/4 meter did learning emerge.

What was the reason for this eventual success? Because of its coincidence for all four pigeons with the change in meter, this seems the most likely cause. It is possible that the change in drum timbres (KS to CT) in the prior phase might have contributed to their improved performance, since the cymbal sound had the broadest frequency range and longest duration of any of the four stimuli (see Fig. 1). If this were the case, the effects of these new sounds were delayed relative to their introduction. Finally, if simple dogged training was at work, it seems very unlikely that it would have occurred coincidentally for all birds at the same point in time. Thus, the change in the construction of the positive meter to increase its discriminabilty was the most likely reason. The key issue now becomes determining the basis for the successful discrimination of the 8/4 and 3/4 meters. Three possibilities need to be considered: rhythmic grouping, timing, and counting. All three are recognized to be involved in human rhythmic behavior.

The first possibility is that sequences were grouped by their rhythmic pattern into auditory segments or phrases in a manner similar to human meter perception. This would require some kind of gestalt perception of each measure as a psychological group. It is possible that the birds heard the meters in that way, although this would not explain why it was so difficult for them to learn during the earlier portions of the experiment. Before any claim of rhythmic grouping might be accepted, however, it is necessary to rule out control by possibly simpler mechanisms related to timing or counting.

A second possibility is that the pigeons had learned to time different portions of each metric pattern, such as the differences in time intervals between the distinctive first beat of each meter. In this case, the pigeons would have learned that "quickly" repeating first beats yield no reinforcement, while longer intervals do. It has been shown that pigeons are capable of timing intervals of this duration with visual and auditory stimuli, although the timing of tones may be less accurate (Roberts et al., 1989). This potential difference between the two modalities may have contributed to earlier difficulties in learning the meter discrimination because of the smaller time differences involved. The results of the single stimulus tests offer some support for a timing account. Some of the pigeons were able to perform the task with just the cymbal at least as well as with both sounds, suggesting that this component was at least sufficient for discrimination. This timing alternative thus suggests the meter discrimination might have been reduced to essentially a tempo discrimination involving the relative timing of the cymbal-defined beat one.

A third possibility is that they learned to count the number of beats between beat one. It has been found that pigeons can count light flashes of quantity and can determine the relative frequency of visual events (Keen and Machado, 1999; Roberts et al., 1995). With the multiple tempos used in Phases 1 and 3, such counting would have been more beneficial as the birds could not have relied solely on relative timing in those cases. The results of the single stimulus test offer little support for a counting alternative, however, since the pigeons were at chance with the tom only trials (xT) that would have been revealed by such counting. The birds could have also relied on the frequency of the rest (silence) in place of the cymbal to accurately discriminate these test trials, but this seems unlikely since such rests were not critical during training. Overall, their general lack of success with multiple tempos suggests that neither counting nor grouping were preferred strategies, leaving the timing/tempo account as the likely best explanation of the discrimination observed in Phase 6.

4. Experiment 2 – extensions

The main goal of Experiment 2 was to create and test a generalized meter discrimination. Such a discrimination would help to better discern the relative contributions of rhythmic grouping, timing, and counting in the discrimination established during the latter portions of Experiment 1. Towards this goal, Experiment 2 involved several different manipulations.

The first part of the experiment expanded the number of stimuli tested with the 8/4 and 3/4 meters. Showing that different types of stimuli could support the same meter discrimination would be consistent with a generalized capacity for this type of discrimination. Thus, we re-introduced the KS sounds back into training, now using the greater meter difference that was successful with the CT stimuli (i.e., KS8+ vs. KS3−). With the greater difference between the lengths of the positive and negative meters the pigeons might generalize their CT discrimination to these familiar stimuli.

Because any true meter discrimination should generalize across tempos, we also tested the CT stimuli with novel tempos in Experiment 2. After this, we then trained the meter discrimination using these new tempos with both the CT and KS stimulus sets. This training was designed to assess whether changes in tempo might also help with the KS discrimination, which had not been learned by this time.

Finally, we tested and trained the pigeons with all 12 permutations of the four stimuli forming the two meters. The goal of this phase was to examine if the pigeons could extract the different meters when the sounds of the first and subsequent beats were counterbalanced across the different sounds and the value of beat one had to be discerned from events within a trial. This kind of flexibility would further speak to the generality of any observed discrimination.

5. Method

5.1. Animals and apparatus

The same pigeons and apparatus were used as in the previous experiment.

5.2. Procedure

5.2.1. Phase 1

This phase reintroduced the KS stimuli using the 8/4 and 3/4 meters. Each session consisted of 96 randomly ordered trials (24 CT8+/24 CT3− and 24 KS8+/24 KS3−) tested at a tempo of 180 bpm. Two probe trials for each stimulus set were tested during each session. Other aspects of the trial organization were the same as at the end of Experiment 1. Twenty sessions using this organization were conducted.

5.2.2. Phase 2

In Phase 2 the pigeons were tested for tempo generalization with the CT stimuli. Four novel tempos (140, 160, 200, and 220 bpm) that were faster and slower than the baseline 180 bpm were tested. These tempo generalization sessions consisted of the 96 baseline trials from Phase 1 plus four probe trials using the CT stimuli testing the novel tempos. Two novel tempos were tested each session with each meter, thus all tempos were tested every two sessions. Sixteen sessions using this organization were conducted. We proceeded to train the pigeons with all five tempos using both CT and KS stimulus sets. These sessions now consisted of 100 trials (25 CT8+/25 CT3− and 25 KS8+/25 KS3−) with each stimulus set tested five times with each tempo. One probe per tempo was tested each session. Twenty-five sessions using this organization were conducted.

5.2.3. Phase 3

In this phase, the pigeons were tested with the 10 remaining pairs of stimulus set permutations (CK, CS, TC, TK, TS, KC, KT, SC, ST, SK) in a series of probe trials. Each session consisted of the 96 baseline trials from Phase 1 plus 10 probes. In each session, half of the 10 were tested with each meter (i.e., if TC8 was tested, TC3 would be tested in the same session). Eight sessions were tested, so each novel stimulus pair was tested a total of four times.

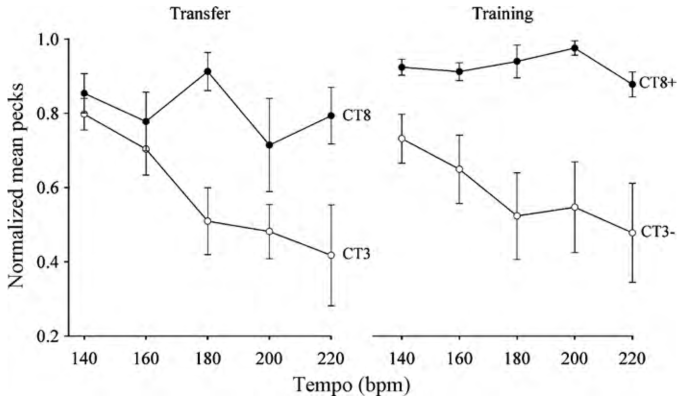

Fig. 4. Mean normalized pecks for all birds across five different tempos during the tempo generalization test (left panel) and subsequent training phase (right panel) of Experiment 2 for the CT stimulus set. Error bars show the SEM.

All 12 stimulus permutations of the four drum sounds were then incorporated into training using the 8/4 and 3/4 meters. These meters and sounds were tested at three different tempos: 140, 180, and 220 bpm. Each session consisted of 144 trials (72 S+/72 S−). Each of the 12 permutations was presented four times per session, twice per meter at all three tempos. A randomly selected 12 of the 36 possible S+ trials were tested as probes each session. Thus, after 60 sessions, at least 17 probes of each combination of tempo and stimulus permutations had been collected from each pigeon.

5.3. Results

5.3.1. Phase 1

Even when tested with the successful 8/4 vs. 3/4 meter discrimination, the KS stimuli failed to support transfer or learning over the first 20 training sessions (mean DR = .51). A repeated measures ANOVA (5-Session Block) using DRs of just KS trials revealed no significant effect of block, *F*(3,9) = 1.4. Over this same period, performance with the already learned meter discrimination using the CT stimuli was maintained. Across all 20 sessions, paired t-tests revealed significantly greater pecking during CT8+ (*M* = 30.7) than on CT3− trials (*M* = 22.7), *t*(3) = 4.1. T-tests involving the individual birds over these 20 sessions revealed that all the birds performed significantly better than chance during this phase with the CT stimuli, *ts*(19) > 2.7 (mean DRs: #1B, .63; #2C, .60; #3J, .56; #4L, .53).

5.3.2. Phase 2

The majority of the pigeons successfully transferred their meter discrimination to faster novel tempos (200 and 220 bpm), but not to the slower ones (140 and 160 bpm) with the CT stimuli. Presented on the left side of Fig. 4 are the mean normalized pecks for each tempo during this generalization test (pecks were normalized to each bird's highest peck rate in any condition). A repeated measures ANOVA (Meter × Tempo) of these normalized peck rates revealed both a significant main effect of meter, *F*(1,3) = 24.4, reflective of discrimination, and tempo, *F*(4,12) = 4.04, but no interaction of these factors. Individually, however, the pigeons showed better transfer to the two faster tempos, especially pigeons #1B, #2C, and #3J. At the slower tempos, these pigeons showed a reduced capacity to perform the discrimination. Pigeon #4L, with a weak discrimination to begin with, maintained his DR across all tempos. Repeated measures ANOVAs (Meter × Tempo) using normalized peck rates from the eight two-session blocks of testing confirmed that #1B and #2C both had significant main effects of meter, *Fs*(1,7) > 44.9, but also interactions with tempo, *Fs*(4,28) > 3.7. The other two birds also had significant effects of meter, *Fs*(1,6) > 5.9, but no significant interaction with tempo, *Fs*(4,24) < 1.

Because of this partial transfer across tempo changes, we introduced the four tempos into training to see if they might help to facilitate KS performance, which had continued to be poor. The latter did not happen as performance continued at chance across all tempos for these two stimuli. Mean peck rates averaged across all tempos remained identical for the KS8+ (*M* = 23.7) and KS3− (*M* = 24.5) conditions. Using just the KS stimuli, a repeated measures ANOVA (5-Session Block × Tempo) of DRs revealed no evidence of learning across blocks, *F*(4,12) < 1 and there was no interaction with tempo *F*(16,48) = 1.54.

In contrast, differential training facilitated performance with the CT stimuli at the different tempos relative to their introduction. The improved discrimination at all tempos can be seen on the right side of Fig. 4 where the difference between the two conditions is larger than that seen in the prior transfer test. All of the birds were now successfully discriminating all of the tempos. A two way repeated measures ANOVA (5-Session Blocks × Tempo) of DRs revealed a significant effect of tempo, *F*(4,12) = 3.6. A series of t-tests comparing peck rates between the two meters at each tempo confirmed the significant CT meter discrimination by all birds across all tempos.

5.3.3. Phase 3

The 10 novel stimulus permutations failed to support above-chance discrimination during the transfer test. Paired t-tests comparing mean peck rates to the two meters for each permutation revealed no significant differences. Introducing all stimulus permutations into training in an attempt create a generalized meter discrimination resulted in an extended period of poor discrimination, where even the established CT meter discrimination collapsed within several sessions. Despite extensive training, we found no improvement in performance. Single mean t-tests comparing individual mean DRs for each stimulus pair over the last 20 sessions revealed the absence of any significant discrimination at above chance levels. A two way repeated measures ANOVA (Meter × Permutation) of peck rates over these 20 sessions showed neither effects of meter, *F*(1,3) = 1.2, nor permutation, *F*(11,33) < 1.

5.4. Discussion

The results of Experiment 2 were mixed. Overall, the pigeons showed no capacity to form a generalized meter discrimination. When tested either with a familiar set of stimuli (KS) or with all permutations of the stimuli, we found no evidence that the prior CT meter discrimination extended much beyond what we observed in Experiment 1. The one positive result to emerge from the experiment was that the CT discrimination generalized to new tempos, principally to those that were faster than that experienced in training.

Again, the issues of auditory grouping, timing, and counting raised by the pigeons' success in Experiment 1 must be addressed with regards to the tempo generalization observed here. It was suggested in Experiment 1 that the successful discrimination of the two meters may have relied upon the relative timing of the cymbal stimulus. During the transfer trials with the faster or slower tempos in Experiment 2, the timing of this interval would have been ineffective, especially given the randomized mixture of the tempos across trials. The better performance with faster tempos is consistent with the hypothesis that auditory grouping might have been promoted by the faster presentation rates. It is also possible that the pigeons were using a counting mechanism, in addition to the timing, which could have also been responsible for the observed generalization.

Past research has indicated that pigeons are able to both time and count a series of light flashes (Roberts et al., 2000). In their study, although they could use both strategies to gain reward after a fixed period of time or a fixed number of flashes, their responses indicated that they continued to time while asked to count, but did not count while asked to time. If this process extends to the auditory domain, the present results could represent a similar combination of these two mechanisms. The one problem with a counting mechanism is that the birds were best with faster tempos, when one would think that slower tempos would be easier to count.

Regardless of the method used, the pigeons again had no success in performing this discrimination with the kick and snare drum sounds, either in isolation or in combination with the cymbal and tom sounds during Phase 3. The pigeons' success at discriminating CT relative to KS may have been due to the distinctiveness of the former sounds. While the kick and snare sounds were qualitatively different to human ears, the cymbal and tom sounds were more distinct. If the pigeons were indeed counting or timing specific stimuli within a measure, such distinctiveness would be vital. However, this distinctiveness did not carry over to the situation where we tested all permutations of these four sounds. In fact, in this case even the successful CT discrimination disappeared within a few sessions.

As best determined here, the pigeons showed little capacity to perform generalized meter discriminations. Their learning seemed to be restricted to a limited set of circumstances, and even that may have been fragile. Even so, simpler mechanisms, like timing and counting, seem to provide adequate alternatives to an auditory grouping hypothesis. Perhaps a different order of training with faster tempos and even more distinctive stimuli might have been more successful. For the moment, the combined results of Experiments 1 and 2 suggest that meter discriminations are difficult for pigeons. While implicitly appreciated by humans, meter discriminations represent a form of advanced rhythmic behavior. With their isochronous beat structure, such discriminations rely on the relational perception of the accented and unaccented beats for any auditory grouping. Perhaps the pigeons' difficulties stem from not being able to appreciate these relations, and so they turn to using timing or counting to solve such problems.

6. Experiment 3 – rhythmic vs. arrhythmic discrimination

At this point, we decided to try a different approach to investigating their appreciation of rhythm. Another critical component of rhythm discrimination is determining whether the interval between two beats is periodic or not. In this next experiment we examined the role of beat isochronicity in the perception of rhythmic structure by pigeons. Again, little animal research on this aspect of rhythm has been conducted (Fay, 1994; Hulse et al., 1984). Hulse et al. (1984) have found that starlings could discriminate between rhythmic and arrhythmic sound patterns. Using 100 ms 2000-Hz tones, their birds discriminated between sequences with isochronous inter-onset interval vs. those that randomly varied between 30 and 300 ms. After readily learning this rhythmic vs. arrhythmic discrimination, it was maintained across a range of tempo changes that halved or doubled the training value.

In this experiment, we tested the pigeons in a similar discrimination between conditions containing isochronous beat intervals (S+, rhythmic) and non-isochronous beat intervals (S−, arrhythmic). Given their difficulties in Experiment 1, we decided to use the rhythmic pattern as the S+ condition to take advantage of any experience that might have accrued from the earlier training. We used the same four drum sounds tested in Experiment 1. Because this discrimination did not require pairs of stimuli, any problems related to their discriminability relative to each other should not be an issue here.

7. Method

7.1. Animals and apparatus

The same pigeons and apparatus were used as in Experiments 1 and 2.

7.2. Procedure

The pigeons were required to discriminate rhythmic and arrhythmic patterns during each session. Each trial used one of the four drum sounds (C, T, K, and S) that were previously used in Experiments 1 and 2. After a peck to the ready signal, each sound presentation lasted 20 s. The isochronous rhythmic pattern was the S+ condition for all pigeons and reinforced on a VI-10 schedule. They were also given 2-s response-independent access to grain following the end of each S+ trial. Pecks to the arrhythmic pattern were not reinforced and resulted in a 1 s per peck timeout in the dark after the trial ended (maximum = 120 s).

7.2.1. Phase 1

The rhythmic and arrhythmic patterns in Phase 1 were created using four tempos (100, 120, 140, and 180 bpm). The rhythmic patterns consisted of a drum sound played at isochronous beats throughout the duration of its presentation. This resulted in inter-onset intervals (IOIs) of 600, 500, 428, and 333 ms for each tempo, respectively. The arrhythmic patterns consisted of a drum sound played at randomly varying non-isochronous beats throughout the duration of its presentation. These non-isochronous values were derived by randomly selecting IOIs from a 50% range on either side of the isochronous value for each tempo. This resulted in a range of IOIs of 300–900, 250–750, 215–644, and 167–500 ms for each tempo, respectively. The different drum sounds were equated by shortening each to 166 ms in duration so that all sounds would fit within the shortest possible IOI. Each session consisted of 128 randomly ordered trials (64 rhythmic S+/64 arrhythmic S−). Each tempo and drum sound was tested an equal number of times within each of these conditions. Four probe trials were conducted with each tempo; one for each different drum sound. Twenty-five sessions using this organization were conducted.

7.2.2. Phase 2

Because no evidence of learning was present after this period of time, several changes were made in Phase 2 to make the discrimination potentially easier. First, only the previously successful C and T stimuli were tested. Second, the two faster tempos were eliminated. Third, the range of IOIs was increased to 75% of the rhythmic value: 150–1050 ms for 100 bpm, and 125–875 for 120 bpm. This necessitated reducing the stimulus duration to 125 ms. Fourth, arrhythmic trials (S−) were programmed to continue playing until the pigeon stopped pecking for at least 3 s in order to encourage learning. The maximum trial length was set to 80 s and a 1 s per peck timeout (maximum = 120 s) still followed S− trials. Each session consisted of 128 randomly ordered trials (64 rhythmic S+/64 arrhythmic S−), with the now reduced number of tempos and drum sounds tested equally often. Two probe trials were conducted with each tempo; one for each different drum sound. Fifteen sessions using this organization were conducted.

7.3. Results

The pigeons had no success in discriminating the rhythmic and arrhythmic patterns. During the 25 sessions of training using the four different tempos and sounds, there was no evidence of discrimination in terms of mean pecks per trial comparing the rhythmic ($M = 23.07$) and arrhythmic ($M = 23.05$) conditions. A repeated measures ANOVA (5-Session Block × Tempo) of DR yielded no evidence of improvement across Blocks for any of the tempos.

Despite the changes made in Phase 2 to simplify the discrimination, the pigeons continued to show no capacity to learn this discrimination. Across these sessions, mean pecks per trial for the rhythmic ($M = 20.3$) and arrhythmic ($M = 20.4$) conditions remained identical. A repeated measures ANOVA (5-Session Block × Tempo) of DR yielded no evidence of improvement across Blocks during this phase of the experiment.

7.4. Discussion

The pigeons showed little ability to learn this form of rhythmic discrimination. Because there was no meter in this experiment, all that was required here was a determination of whether the interval between the onset of the sounds was periodic or not. While counting would have been useless, this discrimination could have been done with a timing mechanism that compared the intervals among three successive sounds. Although not as widely investigated as longer temporal durations, timing studies with single stimuli indicate that pigeons can time such durations (Fetterman and Killeen, 1992). Despite this, the pigeons failed to this learn this discrimination.

These pigeon results stands in contrast to Hulse et al.'s (1984) results with starlings. Besides the obvious species difference, there were also differences in the sounds used and the number of tempos and sounds employed during training. Hulse et al. used only a single tone stimulus for their training, while we used four and then two different four percussive sounds intermixed within a session. Hulse et al. also used only a single tempo during training, while we employed multiple tempos. Our motivation for including these multiple components was to try and establish a generalized discrimination of the sound patterns. This increased auditory complexity, however, may have only served to prevent the pigeons from learning the discrimination as easily as the starlings.

Another caveat that should be kept in mind concerns potential interference effects between the different experiments. Given their experimental history with isochronous meter discriminations, these pigeons may have been hindered by continued attempts to identify a single timbre to either time or count rather than attend to the intervals between the stimuli. Listening for the accent or the odd-sounding beat in order to group sequences was impossible in this experiment, possibly leading to confusion. While the same sounds were played as in the previous experiments, their duration was markedly shorter, which preserved their attack but not their decay. Further, their history with isochronous stimuli may have reduced the salience of this aspect of the sound patterns. Finally, we were not as persistent with this discrimination as with the meter discrimination. Perhaps with more training, the pigeons would have eventually been successful. Future research on this rhythmic discrimination should employ experimentally naïve birds and start with training conditions more similar to those of Hulse et al.'s (1984) in order to better understand whether or not pigeons can discriminate between rhythmic and arrhythmic auditory sequences.

8. Experiment 4 – tempo discrimination

Given the outcomes of the three previous experiments, we decided in the fourth experiment to try yet a simpler form of rhythmic discrimination. Because it is fundamental to rhythm, tempo has been considered an auditory primitive (Hulse et al., 1992). Within the limited literature on rhythmic discrimination in animals, it appears that tempo discriminations are relatively robust

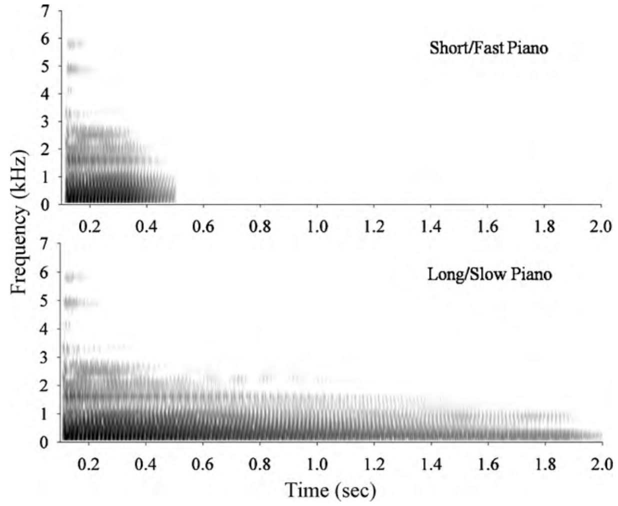

Fig. 5. Spectrograms of the two piano sounds tested in Experiment 4.

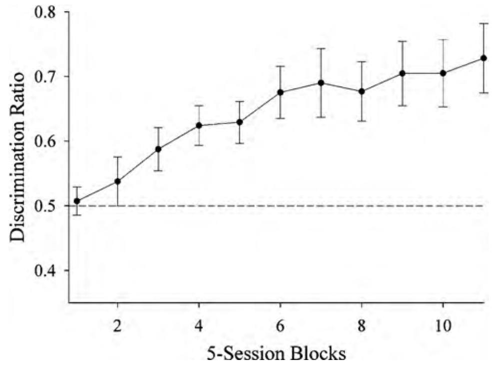

Fig. 6. Mean discrimination ratios for all birds during the acquisition phase of Experiment 4. The dotted line indicates chance performance. Error bars show the SEM.

over a variety of species and procedures (Hulse and Kline, 1993; McDermott and Hauser, 2007; Schneider and Lickliter, 2009). Thus, we assessed the pigeons' ability to discriminate the relative tempo of periodic sounds.

In Experiment 4, the pigeons were required to discriminate between fast and slow repetitions of the same sound. This tempo discrimination allowed us to bring back isochronous intervals for all the stimuli, making it more similar to the partially successful Experiment 1. Because of the concerns over the extensive history accrued to the percussive stimuli in the first three experiments, we also decided to use a novel sound for this experiment. This was a low C piano sound that after its initial attack diminished in intensity proportional to its duration (see Fig. 5).

9. Method

9.1. Animals and apparatus

The same pigeons and apparatus were used as in the previous experiments.

9.2. Procedure

9.2.1. Training

The pigeons were tested with 20 s presentations of repeating auditory stimuli presented at either 120 bpm (S+) or 30 bpm (S−). The repeating stimulus was a low C (130.81 Hz) synthetic piano sound (Garageband, Apple Computer, Inc; Cupertino, California). For the 30 bpm condition the duration of the note was 2 s, while for the 120 bpm condition it was 0.5 s in duration. Following their initial attacks, sound intensity diminished proportional to its duration. All pigeons were reinforced (VI-10 schedule) for pecking during the presentation of the faster auditory sequence. Pecks to the slower tempo resulted in a 1 s per peck dark timeout after the trial terminated (maximum = 120 s). Sessions consisted of 96 randomly ordered trials (48 S+ fast tempo/48 S− slow tempo). Four randomly selected probes of the fast tempo trials were conducted each session. The pigeons were tested for 55 sessions with this organization.

9.2.2. Tempo transfer test

After the discrimination was stable at approximately Session 26, the pigeons were tested with 11 novel tempos (10, 20, 60, 80, 100, 140, 160, 180, 200, 220 and 240 bpm). These sessions consisted of the 96 baseline trials plus either four or five additional non-reinforced probe tests testing randomly selected novel tempos. Thus, it took three sessions to collect a full set of data on all tempos. Nine sessions using this organization were conducted.

9.3. Results

In comparison to the earlier experiments, the pigeons readily acquired this tempo discrimination, showing evidence of discrimination within 15 sessions and steadily improving after that (see Fig. 6). A repeated measures ANOVA (5-Session Block) using DRs revealed a significant effect of block, $F(10,30) = 10.5$, confirming that learning occurred. All birds individually showed significant differences in pecks between fast and slow tempos in t-tests over the last 10 sessions of training for each bird, $ts(9) > 4.3$. Three of the pigeons were quite good at the task, but the one bird, #4L, who had been consistently the poorest throughout all the experiments, still struggled even in this task.

Fig. 7 shows the mean results of the tempo generalization test for each pigeon. Data from the three pigeons that showed good transfer to the novel tempos were analyzed. They classified tempos of 100 bpm or faster as "fast," and tempos of 30 bpm or slower as "slow." The tempos of 60 and 80 bpm supported intermediate peck rates. A repeated measures ANOVA of tempo based on peck rate confirmed the significant main effect for this manipulation, $F(12,36) = 2.8$. Bird #4L showed a small degree of control by the novel tempos, but the poor quality of his baseline discrimination made any strong conclusions difficult for this specific animal.

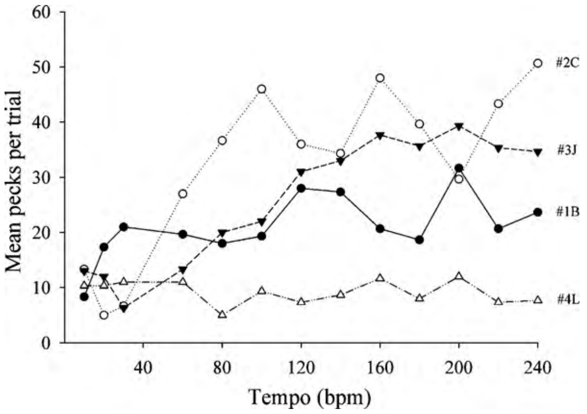

Fig. 7. Mean pecks for each bird during the tempo generalization test of Experiment 4. Error bars show the SEM.

9.4. Discussion

Unlike the previous forms of rhythmic discriminations tested, the pigeons easily acquired this tempo discrimination, pecking when they heard quickly repeating stimuli and inhibiting pecks to the slowly repeating stimuli. Further, this tempo discrimination transferred appropriately to novel slow and fast tempos. The ease of this tempo discrimination increases the likelihood they had acquired the original meter discrimination in Experiment 1 primarily using the same kind of relative timing cue.

Two properties of the auditory sequences could have contributed to the birds' success. The most obvious is the difference in repetition rate of the periodic sounds. This would be consistent with the hypothesis that this aspect of auditory stimulation is a primitive. It would also be consistent with the proposed explanation for the discriminations observed in Experiment 1 based on the relative timing of the accented sounds. While the form of each note was the same across tempos, the duration of the stimuli in the present discrimination was confounded with it. We chose to do it this way because using sounds of equivalent duration would have resulted in differential durations of silence between each sound. To our ears at least, having the sounds be continuous better emphasized the tempo of the sequences. The duration of the stimuli appears not to be important, however, as we have conducted subsequent studies using stimuli of equivalent duration that indicate the rate of presentation is the most critical factor in these types of sequences.

Another factor that may have contributed to their success in this tempo discrimination might be linked to the introduction of a new sound that may have been more salient or audible. Given what is understood about the processing of auditory sounds by pigeons, however, it is not obvious why this should be the case. Finally, in this experiment we synchronized the different tempos with the discriminative response, so that fast peck rates were required for fast tempos and slow peck rates for slow tempos. It will be interesting in future research to see if this isomorphic mapping of response rate to stimulus rate may have also contributed to the ease of the current discrimination compared to the non-isomorphic meter discriminations in Experiments 1 and 2.

10. General discussion

These experiments tested pigeons with various forms of rhythmic discriminations. Overall, the pigeons appear to be capable of learning rhythmic discriminations that relied on relative timing or tempo of the periodic stimuli. Beyond that, they seem to have more difficulties in learning other forms of rhythmic discriminations. The pigeons failed to learn a generalized discrimination between rhythmic and arrhythmic patterns of sounds involving different tempos. Although not easily learned, under some circumstances the pigeons were able to acquire a meter-like discrimination that generalized to faster tempos. However, this meter-like discrimination was not robust when challenged with a wider variety of stimuli. These data would suggest that the discrimination of rhythmic auditory patterns, as broadly implemented in these various tasks, is not a well developed capacity in pigeons beyond the determination of tempo.

Given the mixture of success and failures in these tasks, what mechanisms best account for these results? Earlier we considered three mechanisms intimately involved with the perception of rhythm: timing, counting, and rhythmic grouping. Overall, the results of these experiments suggest that a form of interval timing was an important contributor to the pigeons' ability to discriminate among these periodic auditory patterns. The rapid discrimination of fast and slow tempos in Experiment 4 certainly indicates a strong sensitivity to periodic time. Further, we think the meter discrimination results of Experiment 1 can be reduced to a form of periodic timing as well. These results suggest that pigeons have the capacity to discriminate temporal intervals when marked by periodic stimulus events over the millisecond to multi-second range. Although not as widely investigated as longer temporal durations, standard timing studies with visual stimuli indicate that pigeons can time across that range (Fetterman and Killeen, 1992). Why this same mechanism would be insensitive to timing the randomly varying non-isochronous intervals in Experiment 3 is a bit of mystery. Perhaps periodicity is somehow critical to the accurate functioning of this kind of timing mechanism (Keele et al., 1989; Schulze, 1978).

The best evidence that event quantity played a role in these experiments comes from the transfer to novel tempos in Experiment 2. Given its metrical structure, these changes in tempo made interval timing far less useful than when only one tempo was used during Experiment 1. Yet at least for faster tempos, the pigeons clearly transferred the discrimination. These data suggest that they were likely sensitive to the quantity of unaccented beats provided by the tom stimulus in addition to the rate of cymbal repetition. Thus, perhaps a combination of timing and quantity cues were employed in some cases. Pigeons have been shown to simultaneously time and count series of light flashes (Roberts et al., 2000). If this dual mode processing were also available in the auditory modality, it could account for the successful tempo discriminations and transfers observed here.

One possible reason the pigeons had greater skill timing periodic rates in Experiment 4 might be tied to aspects of their natural vocalizations. The measure of event frequency or tempo is in many ways similar to the dimension of intensity. Pigeons might be sensitive to the rate or tempo of auditory stimulation because this is important to how they naturally communicate. As mentioned in the introduction, pigeons have an unlearned vocabulary of about five basic, often repetitive, vocalizations. Their frequency, intensity, and duration are important cues for pigeons and doves in helping to differentiate between aggressive and appetitive states (Rashotte et al., 1975; Slabbekoorn and ten Cate, 2001). While the rates and intensities tested here were different than typically experienced with vocalizations, the importance of this natural periodic information may provide the foundation for the strong temporal control observed here with unnatural stimuli.

Another key mechanism for any form of rhythmic discrimination is a working memory that allows auditory information to be maintained and compared to determine whether there are sequential patterns present (Snyder, 2000). Each of our discriminations required detecting auditory patterns over the time range of milliseconds to seconds. While pigeons have a visual working memory that clearly lasts for a number of seconds, one possibility is that their auditory short-term memory is not as strongly developed. Studies of DMTS performance with pigeons have reported slower acquisition with auditory sample stimuli than with visual sample stimuli (Kraemer and Roberts, 1984). Roberts et al. (1989) have found that pigeons are not as accurate at timing tone stimuli than visual stimuli. Cook and Brooks (2009) found that pigeons needed to hear more sounds to successfully perform an auditory same/different task than a comparable visual task. Such findings suggest that the sequential processing and retention of auditory information may not be as well developed as visual processing in these birds.

Future research will need to look at a wider variety of species to ascertain the sufficient and necessary neural, ecological, and evolutionary conditions for robust rhythm discriminations. Despite our determined effort to examine the issue of rhythmic processing in pigeons, even here more work is clearly needed. Because we repeatedly used the same pigeons, the potential for order effects needs to be recognized in our research. Would the results have been the same if we tested different groups of experimentally naïve birds in our three discriminations, for example? Perhaps the initial learning of tempo discriminations first could serve as scaffolding for learning more complex rhythmic discriminations involving meter and syncopation. Besides its contributions to the understanding of the cognition and evolution of music, an increased attention to understanding how animals generally process sequential auditory patterns should make important contributions to our understanding of the mechanisms of multi-modal cognitive information integration over time.

Because these experiments were started in part with an interest in understanding how animals might process auditory information within a potential musical context, it is appropriate to briefly return to this topic. The human perception and appreciation of musical rhythm is easy and highly natural. It is often difficult not to tap your foot when hearing a piece of music, particularly if it has a strong metric pulse (Drake et al., 2000; Snyder and Krumhansl, 2001). Rhythm is also important to human language and speech (Kohler, 2009; Patel and Daniele, 2003). It has not gone unnoticed that there may be a relationship between rhythmic processing within the domains of language and music (e.g., Besson and Schön, 2006).

As mentioned in the introduction, Patel has recently theorized that vocal learning is critically tied to the ability to synchronize movements to rhythm (Patel, 2006, 2008). Based on the results of the current experiments, the difficulties that the pigeons have learning various rhythmic discriminations are also consistent with Patel's hypothesis. Furthermore, several analyses looking for temporal patterns in the pigeons' pecking response to the repeated sounds revealed little evidence of such entrainment. Because pigeons do not learn their vocalizations, they may not have the neural and genetic structures necessary to process the underlying pulse of complex auditory patterns like music. Rather, from their perspective, and perhaps for many animals, it is the intensity, frequency, or tempo of auditory events that is most critical for their daily existence. While periodicity may play a role here, it does not equate to appreciating a larger rhythmic structure or grouping. Such features may be unfathomable to a pigeon, thus they could never "appreciate" the different rhythmic expectancies so critical to music and to which humans so strongly resonate. In a manner perhaps analogous somewhat to when we hear a foreign language that we cannot speak (in which we can hear the sounds, but cannot determine where the proper word and phrase boundaries lie), pigeons may not be able to experience the larger rhythmic structures that hold together complex auditory sequences like those found in music. Similar receptive amusia resulting in the loss of rhythmic abilities has been reported in humans (Di Pietro et al., 2004). Jarvis (2007) suggests that, because the auditory pathway is similar in birds, mammals, and reptiles, it was likely inherited from their common ancestor over 300 million years ago. If so, pigeons might be able to appreciate the melodic and harmonic structure of a piece of music and they have shown some potential for doing so (Brooks and Cook, 2010). Nevertheless without a more sophisticated rhythmic comprehension there can be no appreciation of the overarching and necessary structure inherent to music.

Acknowledgements

This research was supported by Grant #0718804 from the National Science Foundation. The authors thank Ani Patel for comments on an earlier version of this manuscript.

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