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An exploration of rhythm perception in African penguins (*Spheniscus demersus*)

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Rhythmic properties in penguin vocalizations may be unique to individuals. Rhythm perception is an ability previously thought to be exclusive to vocal-learning species with neurological complexities allowing them to mimic conspecific and heterospecific vocalizations. Discovering rhythm perception in penguins would provide insight on penguins' ability to recognize kin using auditory cues, and discount theories constraining rhythm perception to vocal-learning animals. The goal of this study was to learn if African penguins (*Spheniscus demersus*) could perceive changes in rhythm using a habituation-dishabituation paradigm. Subjects were 32-38 African penguins housed at the Seneca Park Zoo in Rochester, NY. Penguins were played four rhythms at 4 kHz and head turns per bird were counted in 24 sessions. Each session consisted of ten familiarization trials followed by six test trials that alternated between the familiar and novel rhythm. Head turns per bird did not significantly increase from the last three familiarization trials to the first novel test trial. Results did not provide evidence for auditory rhythm perception in penguins. This may be because of limitations of the method. Another possibility is that the methodology used was not ideal for discovering rhythm perception in penguins. More research on auditory rhythm perception in penguins is needed.



1. INTRODUCTION

Rhythm can be broadly defined as a sequence of sounds with a temporal pattern that repeats over time (Hulse, Takeuchi, & Braaten, 1992; Mercado & DeLong, 2010; Trehub & Thorpe, 1989). Humans and some non-human animals can perceive and/or produce rhythms (Patel, 2006). Rhythm perception or production has been seen in non-human animals both in the wild and in a laboratory setting. For example, in their natural habitats, songbirds and crickets incorporate rhythmic properties into mating rituals (Saar & Mitra, 2008; Wagner & Reiser, 2000). In laboratory studies, rhesus monkeys have been trained to tap rhythmically (Merchant & Honing, 2014), starlings were trained discriminate between multiple rhythmic stimuli (Hulse, Humpal & Cynx, 1984), and bottlenose dolphins have been shown to be able to perceive and produce rhythms (e.g., Harley, Crowell, Fellner, Odell, & Larsen-Plott, 2005; Harley, Odell, Putnam, Goonen, & DeLong, 2002).

The current study examines auditory rhythm perception in the African penguin (*Spheniscus demersus*) using a habituation-dishabituation method. Penguins rely heavily on auditory signals to locate and recognize their kin in large, noisy breeding colonies while other birds are vocalizing, and sound is readily attenuated by penguin bodies (Aubin 2004; Aubin & Jouventin, 2002; Favaro et al., 2015). This makes them a good subject to study for rhythm perception. Penguins use auditory cues to recognize kin (Clark, Boersma, & Olmsted, 2006). The mechanism behind auditory kin recognition in penguins is still unknown, however, it seems rhythm perception may be involved. Penguins have a variety of vocalizations, many of which have stereotypical rhythmic patterns. One penguin vocalization call, the ecstatic display song, has a very distinct rhythm. This vocalization is composed of three syllable types: short syllables, long syllables, and an inhalation syllable (Favaro et al., 2014). Research has shown that variations in the rhythmic structure of this call seem to be unique to individuals (Favaro et al., 2015).

Habituation-dishabituation methods have been used extensively in developmental psychology (for a review see Kavsek & Bornstien, 2010). When something is interesting to infants, they visually fixate on it for longer. When something is no longer interesting to infants, they look at it for less time and turn their head away from the source of the stimulus. This habituation-dishabituation paradigm can also be used to study perception in animals who will, like infants, orient toward a novel stimulus and habituate to a stimulus after repeated exposure. Habituation-dishabituation studies have been used to study auditory perception in both humans (Lipton & Spelke, 2003; Pickens & Bahrick, 1995) and non-human animals (Fischer, 1998; Ramus, Hauser, Miller, Morris, & Mehler, 2000; Svedsen et al., 2012). One unique element of the current study is that it utilized a habituation-dishabituation method to test auditory discrimination in a group of animals rather than with individuals. Although the habituation-dishabituation method has apparently not yet been used on a group of animals, there is evidence that habituation can be seen in groups of animals who have repeated exposure to stimuli. For example, groups of king penguins (*Aptenodytes patagonicus*) have been shown to habituate to the sound of overhead helicopters (Hughes, Walunda, Stone, Ridout & Shears, 2008) and groups of Magellanic penguins (*Spheniscus magellanicus*) were able to habituate to human presence (Fowler, 1999). A key similarity in these studies was that when penguins were attentive and alert, they exhibited head turning, and this behavior diminished over time as habituation occurred. In the current study, the number of head turns per bird was used as a measure of attention in a habituation-dishabituation paradigm designed to investigate penguins' ability to discriminate among pure tone rhythmic stimuli.

2. METHOD

A. ANIMAL SUBJECTS

The subjects were African penguins housed at the Seneca Park Zoo in Rochester, New York. Throughout the duration of the study there were between 32 (16 adult males, 2 juvenile males, 13 adult females, 1 juvenile female) and 38 (16 adult males, 2 juvenile males, 11 adult females, 1 juvenile female, 8 unsexed chicks) healthy African Penguins (*Spheniscus demersus*) present. Subjects included chicks (under three months), juveniles (under one year), and adults (1-23 years). All penguins were born under human care. Subjects were housed in an enclosure composed of two areas. The outdoor habitat on display

to the public had a 56,781 L pool, a beach made of a cement and sand mixture, and tunnels for hiding. The indoor habitat off display from the public had a 1.2 x 1.2 x 1.2 m pool, 10 to 13 dens (varied from day to day), and multiple enrichment devices (e.g., colorful plastic chains hanging from the ceiling, dog toys, rocks stacked in various locations, plastic baby toys). All research sessions with the penguins occurred in the indoor habitat. The dimensions of the indoor habitat are shown in Figure 1.

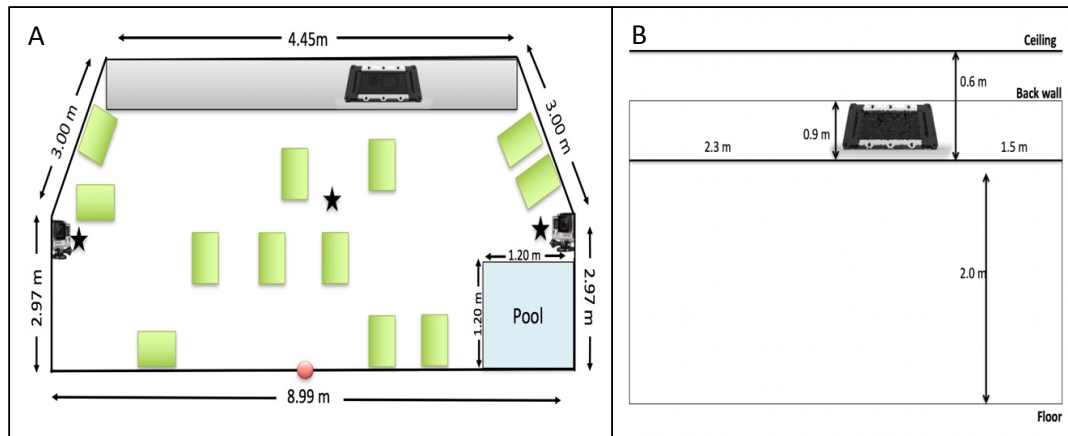


Figure 1. A) A top down representation of the indoor penguin habitat. The pool on the right is 1.2 meters deep and the green rectangles represent the approximate location of the penguins' dens, filled with newspaper litter. The red circle represents where the experimenter stood behind closed doors during sessions. The black stars represent the positions the experimenter recorded sound pressure level measurements at the beginning of each session near each camera. B) The position of the speaker in the penguin habitat.

All subjects were experimentally naïve at the time of the study and the animals' diets were not constrained for experimental purposes. Most penguins were fed twice daily, once between 9:00 am and 10:45 am and once between 2:00 pm and 4:00 pm. Nesting penguins with chicks were fed approximately five times throughout the day. Feeding times varied daily based on the keeper's schedules. Subjects' diets consisted entirely of fish supplemented with vitamins. Penguins were fed silversides (*Menidia menidia*), rainbow trout (*Oncorhynchus mykiss*), and capelin (*Mallotus villosus*). The penguins ate a minimum of four fish a day, and were fed until satiated.

B. MATERIALS

Apparatus

An in-air speaker (FUGOO© Tough) was used to play auditory stimuli. The speaker has a frequency response of 60 Hz to 20 kHz. The speaker also has a battery life of 40 hours and Bluetooth connectivity of up to 10.05 m. The speaker was mounted in the penguin habitat out of reach of the animals, as shown in Figure 1. An Apple iPhone 6 was used to play mp3 stimuli. The experimenter played stimuli on the speaker remotely from the iPhone via Bluetooth connection.

Two Go-Pro© cameras (Hero3+ and Hero 4) were mounted using adhesive 3M© brackets (for positioning of cameras see Figure 1). These cameras were used to capture video footage of all pilot and test sessions. Cameras were positioned above the penguins at opposite ends of the room to capture the entire indoor portion of the penguin habitat. This ensured that all animals that were not in their dens could be seen on camera (for camera points of view see Figure 2). The experimenter was out of sight of the penguins during stimulus presentation and watched penguin behavior through two small windows located in the diet preparation area of the penguin building.

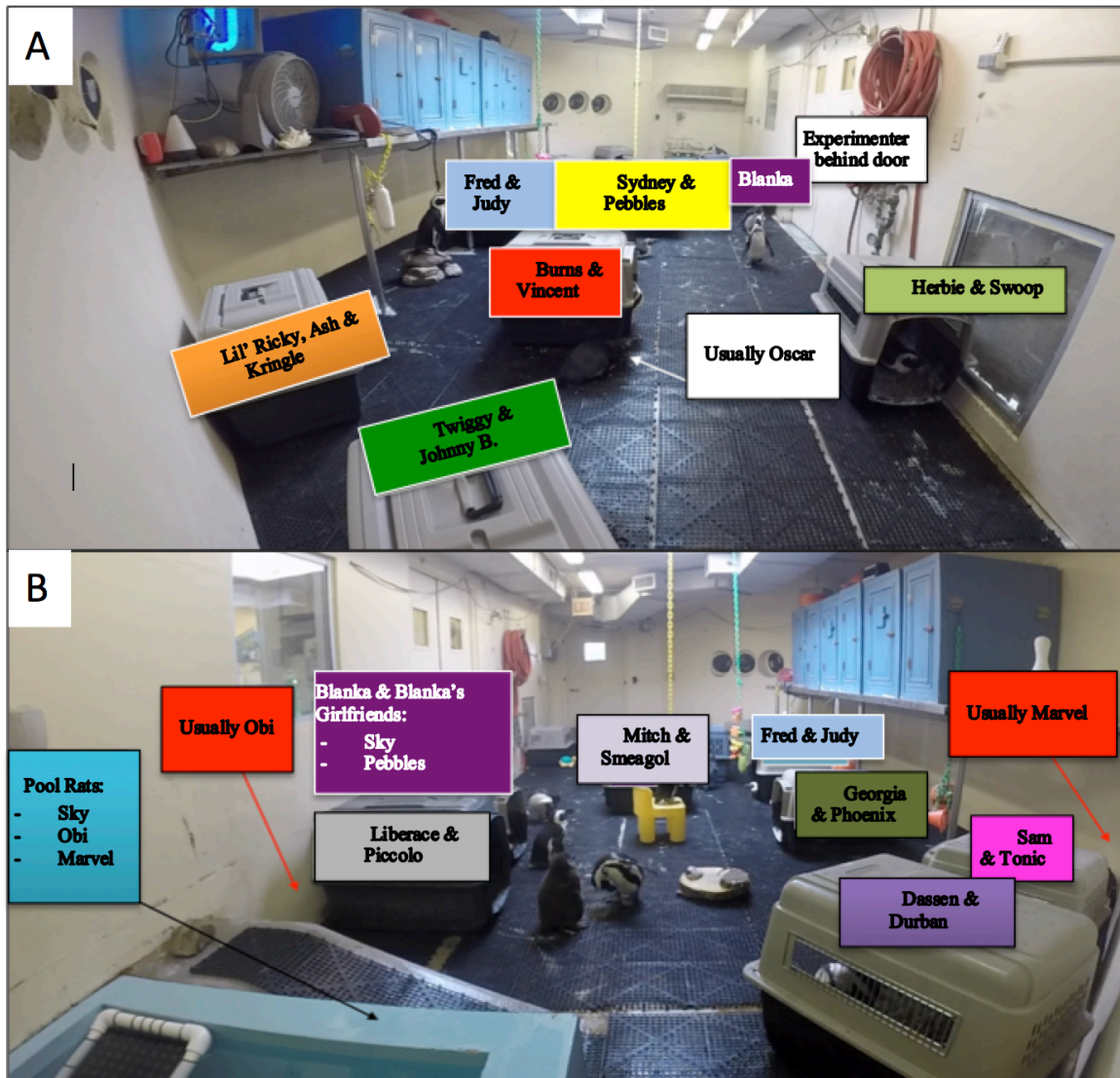


Figure 2. The indoor view of the indoor penguin habitat from A) Camera 1 and B) Camera 2. The labels depict where penguins normally stand during sessions.

Stimuli

Auditory stimuli were generated using Audacity® (2016, Version 2.1.2). All stimuli were created using a pure 4 kHz tone and periods of silence. The frequency of stimuli was selected because African penguins are most sensitive to sounds played at 4 kHz in air (Wever et al., 1969). Stimuli were presented at a tempo of approximately five beats per second (or 2.5 tones per second, excluding inter-tone intervals) which is similar to the vocalization rate of African penguin chicks when peeping (~3.0 tones per second,

excluding inter-tone intervals; Favaro et al., 2014). Stimuli were played at a sound pressure level of 70 dB re 20 μ Pa. A battery powered sound level meter (Tacklife SLM01 Classic Decibel Meter) was used to verify that stimuli were played at a constant sound pressure level at the beginning of each session. The experimenter took dB readings from three fixed locations in the penguin habitat: a central location (1.22 m back and 0.41 m to the right of the speaker), and from the position of each of the two cameras. The three positions where sound pressure level readings were taken are indicated by black stars in Figure 1. In the central location, the sound pressure level was always set to 70 dB re 20 μ Pa. Measurements from the camera locations were always within 2 dB of 70 dB re 20 μ Pa.

Figure 3 shows the stimuli used in the study. One of the sounds presented to subjects was isochronous, meaning all tones and inter-tone intervals were the same duration. The isochronous stimulus consisted of alternating tones and inter-tone intervals of 250 ms. The isochronous stimulus has been used in many studies examining rhythm production (e.g., Hulse et al., 1984). This stimulus is also similar to the rhythm of African penguin chick peeps and moans (Favaro et al., 2014). The “Long/short” stimulus is original and varies from the isochronous stimulus in both tone and inter-tone interval duration. The “Hierarchical” stimulus is adapted from Hulse et al. (1984), and tone lengths are equal to those in the isochronous stimulus, but inter-tone intervals are different. This is to control for the possibility that only tone length, and not rhythm, is controlling the penguins’ behavior. Another stimulus, “Charge”, was adapted from a stimulus used in D’Amato and Salmon (1982). This stimulus was selected because it has tones that vary in duration from the isochronous stimulus and from one another, but the duration of inter-tone intervals is constant throughout the Charge stimulus. This stimulus was used to control for the possibility that only inter-tone length, and not rhythm, could be controlling the penguins’ behavior.

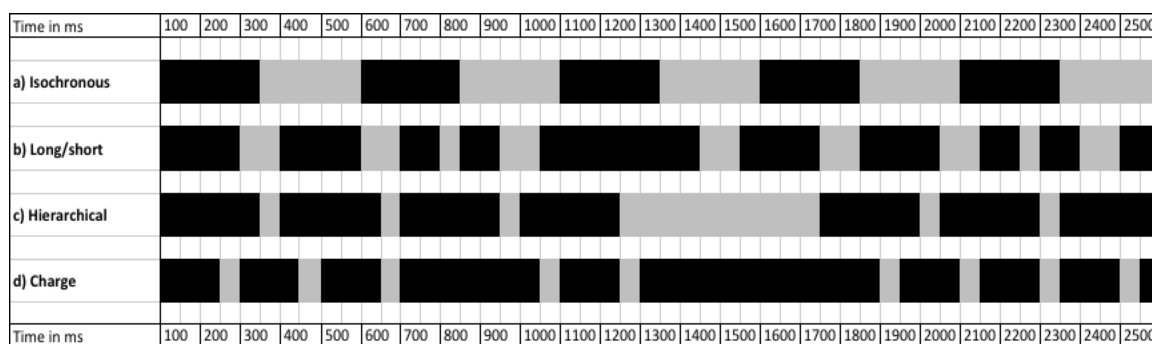


Figure 3. The black bars represent the length of the 4 kHz tone and the grey represents the silent inter-tone intervals of the auditory stimuli that were used in this study.

C. PROCEDURE

i. Pilot Study

The pilot study occurred between November 2016 and January 2017. The main goals of the pilot study were to develop an ethogram of the penguins’ baseline behavior, observe how the animals responded to auditory stimuli, and to determine approximately how long it would take for penguins to habituate to auditory stimuli. The pilot study was composed of three stages.

Stage 1.a. In Stage 1, penguins were observed in their indoor habitat without being presented with auditory stimuli. The purpose of this stage was to habituate birds to equipment, develop an ethogram, and observe baseline behavior. The goal of Stage 1.a. of the pilot study was to set up equipment (cameras) and observe and record penguin behavior in same the location and at the same time test sessions would

eventually occur. During this stage, cameras were positioned and captured footage of the penguins for an hour. The experimenter stayed in the fish preparation area and observed the animals from small windows. The experimenter recorded the animals observed in the given session and notable behaviors to help with animal identification during the session. Later, the experimenter watched the footage and compiled a comprehensive list of animal behaviors and developed an ethogram.

Stage 1.b. Once Stage 1.a. was complete and an ethogram was developed, Stage 1.b. began. The goal of this stage was to observe the penguins and fill out an ethogram to establish baseline behavior. During this stage, one hour of film was recorded from each camera. The speaker was not mounted during this stage. During the session, the experimenter recorded which penguins were present, their behaviors, and the times they occurred in relation to the start of the sessions as landmarks when coding film. Later, when coding the video sessions, an ethogram was used to record the behavior of a focal animals every 30 s in each video. Once the results of the ethogram revealed penguin behavior was similar from session to session (e.g., across sessions focal birds spent most of their time maintaining their feathers or standing, and very little time turning their heads) the speaker was introduced in Stage 1.c.

Stage 1.c. The goal of Stage 1.c. was to habituate the penguins to the presence of the speaker (with no sounds playing). This stage was mostly identical to Stage 1.b., but the speaker was introduced and remained in the penguin habitat for the duration of the session. The cameras and the speaker were placed in the enclosure and then video was recorded for one hour. During the session, the experimenter recorded the penguins present during the session, as well as notable behaviors and the time they occur. An ethogram was used to code the footage collected during sessions. This stage continued for four sessions. The penguins' behavior did not change significantly when the speaker was introduced (see Figure 4). The penguins continued to spend most of their time standing and relatively little time turning their heads. Stage 1.c. was composed of six sessions, three before the introduction of the speaker and three after.

Stage 2. The goals of Stage 2 were to establish an orienting response to auditory stimuli and learn how long it would take penguins to habituate to the carefully selected auditory stimuli that were unlike those to be played during data collection. Four pilot sound types were played in Stage 2: a female voice reading the alphabet, penguins from the Seneca Park Zoo vocalizing, wind chimes, and wild African penguin chicks (unrelated to our subjects) vocalizing. The experimenter played up to three sound types in a session. In each session, each sound was played 5 or 10 times at 70 dB re 20 μ Pa for ten seconds, with either 30 second or 60 second intervals of silence in between stimuli. Video footage from this stage was coded by counting the number of animals turning their heads and the number of animals engaged in other behaviors during the presentation of the pilot stimuli. Stage 2 pilot sessions revealed that head turning was an appropriate orienting response since penguins engage in head turning during the presentation of auditory stimuli. During this stage, which lasted a total of four sessions, the experimenter was also able to observe habituation to the recordings of a female voice speaking the alphabet and Seneca Park Zoo penguin vocalizations (both were familiar stimuli). Birds were considered habituated if the mean total head turns counted in the last three habituation trials had to be at least 50% of the mean total head turns in the first three habituation trials. This is the same criterion used in previous habituation-dishabituation studies (Beier & Spelke, 2012; de Hevia & Spelke, 2010; Pickens & Bahrck, 2011).

Stage 3. The goal of Stage 3 was to determine if penguins would respond to test stimuli as they did to pilot stimuli with head turns as an orienting response. Each test stimulus was played in at least one session. Sounds were played for 10 s with 30 s inter-tone intervals at 70 dB re 20 μ Pa. During this stage, which lasted a total of three sessions, head turning was observed during the presentation of each test stimulus. Only three sessions were run to avoid overexposing the penguins to the test stimuli before the test sessions.

Test Sessions

Data collection consisted of 24 test sessions conducted from January 31st to April 8th, 2017. Each of the four rhythms was used as a familiarization stimulus in six sessions. Each rhythm was paired with every other rhythm (e.g., Charge and Hierarchical, Charge and Isochronous, Charge and Long-Short). Each combination was used in a “familiar first” and “novel first” condition to control for order effects. All experimental sessions occurred between 11:30 am and 1:00 pm, 30 minutes to two and a half hours after the penguins’ morning feeding. Penguins participated in a single experimental session per day and were not reinforced with food during sessions. Sessions were conducted on Tuesdays, Thursdays, and Saturdays.

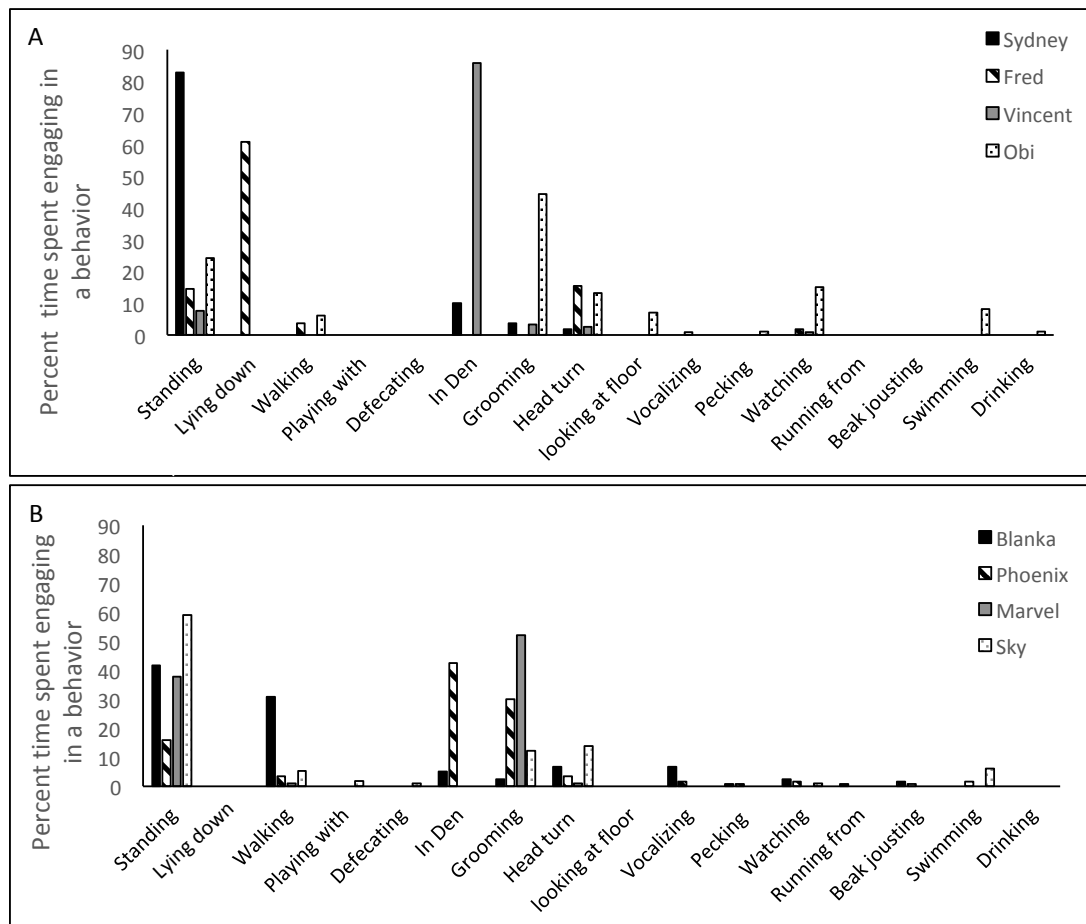


Figure 4. Percentage of time engaged in various behaviors *A*) before the introduction of the speaker and *B*) after the introduction of the speaker in the pilot study. Note that the penguins that were visible in *A* and *B* are not the same animals. The birds observed in this figure were those visible for the entire 30 minutes.

The procedure for each test session included equipment set-up, a waiting period, and sixteen trials. First, the experimenter entered the penguin habitat and mounted the two cameras and speaker (refer to Figure 1). After equipment was set up and dB meter readings were taken, the experimenter waited 25 minutes before beginning a test session to allow the penguins' behavior to return to baseline. Each session began with a habituation period where a test stimulus, deemed the "familiar" stimulus for that session, was played ten times for 10 s with 30 s inter-trial intervals (silence). Following the habituation period, six test trials occurred; three in which the familiar stimulus was played, and three in which a "novel" stimulus, one that the penguins had not yet heard that day, was played. The six test trials alternated between the novel and familiar stimulus.

ii. Video Coding

For each session, the experimenter counted the number of head turns displayed by penguins when sounds were being played. This coding was always done blindly (during coding, videos were muted, so coders did not know which stimuli were playing). When *Spheniscus* penguins and other species of penguins are alert and vigilant, they swivel their heads back and forth to observe their surroundings with one eye, then the next (Eggleton & Siegfried, 1979). Head turns were counted using the same method as Fowler (1999). Each change of the side of a penguin's head was counted as one head turn. Head turns were only counted for animals visible to cameras over the course of the entire session ($n = 4-11$ birds). Before coding, all videos were prepared for coding using Apple iMovie (2017, version 10.1.5). The experimenter time-stamped the points in the video when stimuli were presented in the video, and indicated when to begin and stop counting head turns. All sessions were recorded and scored by the experimenter using consistent criteria.

iii. Inter-rater Reliability

A second coder was hired to code videos to check for inter-rater reliability to control for potential experimenter bias. The second coder coded eight of the twenty-four sessions (about 30% of data). The second coder had no prior experience coding behavioral videos or observing penguins and did not know what predictions were being tested. The second coder attended two training sessions with the experimenter. In the first training session, the experimenter slowly coded a session and explained head turning criteria while the second coder observed. In the second training session, the second coder coded a session slowly, taking time to ask questions from the experimenter, who was observing the second coder closely. The second coder was paid \$10/hour and spent 15 hours coding 8 sessions.

Agreement in the inter-rater reliability check was calculated by dividing the larger total number of head turns in a session for all birds combined (counted either by the first or second coder) by the smaller counted number of head turns. Results for of the inter-rater reliability check revealed 87% agreement over all sessions, and individual sessions had an agreement rate which ranged from 80-98% across seven sessions. An eighth session initially had a low agreement value of 52%. The experimenter recoded this session and found that the disagreement came from an error made by the second coder. The second coder coded a different penguin than the experimenter in attempt to code a penguin referred to as "Unknown Penguin 1". The experimenter recoded the entire session counting head turns for the same "Unknown Penguin 1" as the second coder, which resulted in a 98.94% agreement rate. This eighth session was excluded due to the error made by the second coder.

3. RESULTS

For every session, including all familiarization trials and test trials, the total number of head turns for all birds per trial was divided by the total number of birds present across the entire session because the number of birds visible throughout the entire session varied from session to session ($n = 4-11$). This calculation resulted in a value we will refer to as "head turns per bird" (as in Fowler, 1999). Descriptive statistics were calculated for the average head turns per bird across the final three familiarization trials (trials 8, 9 and 10) and the first novel test trial (trials 11-16), all novel and familiar test trials, and for the average of all novel tests and all familiar tests.

The results are divided into three sections: (1) analyses for the ten familiarization trials, (2) a comparison between the last three familiarization trials and first novel test trial (where dishabituation could occur), and (3) analyses of the six test trials in which the stimulus being played alternated between the novel rhythm and the familiar rhythm.

A. FAMILIARIZATION TRIALS

A habituation criterion similar to those used in previous studies was used to define habituation (Beier & Spelke, 2012; de Hevia & Spelke, 2010; Pickens & Bahrick, 2011). To meet habituation criterion, the mean total head turns counted in the last three familiarization trials (8, 9 and 10) in a session had to be at most 50% of the mean total head turns in the first three familiarization trials (trials 1, 2 and 3). In 9 out of the 24 test sessions, penguins habituated to the familiar stimulus. Penguins did not meet this habituation criterion in 15 sessions.

Unfortunately, there was not an equal number of sessions in which the habituation criterion was met for each of the four rhythm stimuli (isochronous, hierarchical, charge, long-short). Interestingly, penguins did meet the habituation criterion in five out of the six sessions where the Isochronous rhythm was the familiarization rhythm. In contrast, penguins never met habituation criterion in sessions where the familiarization rhythm was Charge and only met habituation criterion in two out of six sessions where the familiarization rhythm was Hierarchical or Long-short.

Another interesting observed pattern was that the average number of birds observed was slightly lower in sessions where birds habituated to the familiar stimuli ($M = 5.78 \pm 1.40$) than when they did not ($M = 7.10 \pm 2.22$). There were also fewer sessions meeting the habituation criterion in the final 12 test sessions (3 sessions) compared to the first 12 test sessions (6 sessions). The penguins met the habituation criterion more often during the first half of the experiment and when there were fewer birds present.

B. TRANSITION FROM FAMILIARIZATION TRIALS TO FIRST NOVEL TEST TRIALS

We compared the end of the familiarization trials (last three trials) to the first novel test trial using a repeated measure analysis of variance (ANOVA) to investigate whether the head turning behavior of penguins changed when the first novel rhythm was played in the test trials (see Figure 5a). All p -values were adjusted using Holm's method for multiple comparisons (Holm, 1979). A 2 (habituation condition: habituation criteria met, habituation criteria not met) \times 2 (trial type: average of last three habituation trials, first novel test trial) \times 4 (familiarized rhythm: Charge, Hierarchical, Isochronous and Long-short) ANOVA was conducted on number of head turns per birds across all sessions ($N = 24$).

Contrary to expectations, the ANOVA revealed no statistically significant main effect of trial type, $F(1, 42) = 5.00$, $p > 0.05$. The average number of head turns per bird for the final three familiarization trials ($M = 0.90$, 95% $CI = 0.72, 1.09$) was not significantly different than the average number of head turns per bird for the first novel test trial ($M = 1.18$, 95% $CI = 1.00, 1.37$). The penguins did not turn their heads more when presented with a novel rhythm after hearing a familiar rhythm for ten trials (see Figure 5a). The ANOVA also revealed no significant main effect for habituation condition, $F(1, 42) = 0.05$, $p > 0.05$. The average number of head turns per bird was not significantly different in sessions where the habituation criteria was met ($M = 1.06$, 95% $CI = 0.82, 1.31$) than when it was not met ($M = 1.03$, 95% $CI = 0.85, 1.65$). Penguins in sessions considered to be habituated to the familiar rhythm did not turn their heads more often upon first presentation of the novel rhythm compared to sessions where they did not habituate. Finally, the ANOVA showed no significant main effect for familiarization rhythm, $F(3, 42) = 2.22$, $p > 0.05$. There were no significant differences in average number of head turns per bird among sessions beginning with each of the four rhythm stimuli: Charge: $M = 1.18$, 95% $CI = 0.70, 1.66$; Hierarchical: $M = 0.85$, 95% $CI = 0.43, 1.26$; Isochronous: $M = 0.91$, 95% $CI = 0.47, 1.36$; Long-Short: $M = 1.24$, 95% $CI = 0.82, 1.65$. The nature of the familiarization rhythm did not impact the number of head turns per bird in the first novel test trial.

C. TEST TRIALS

A second repeated measures ANOVA was used to analyze average head turns per bird across the six test trials. Again, all p -values were adjusted using Holm's method for multiple comparisons. A 2

(habituation condition: habituation criteria met, habituation criteria not met) x 3 (test trial order: first pair, second pair, third pair) x 4 (familiarization rhythm: Charge, Hierarchical, Isochronous and Long-short) x 2 (trial type: Novel vs. Familiar) ANOVA was conducted on head turns per birds across the three sets of test trials.

There was no main effect of trial type, $F(1, 136) = 0.53, p > 0.05$. The penguins did not turn their heads more often on novel trials compared to familiar trials. There was also no significant main effect of test trial order, $F(2, 136) = 0.50, p > 0.05$. The penguins did not change their head turning behavior throughout the test trials. The results of the ANOVA also revealed no significant main effect for habituation, $F(1, 136) = 1.03, p > 0.05$. Meeting habituation criteria (or not) during the familiarization trials did not change their head turning behavior throughout the test trials. Finally, the ANOVA showed no significant main effect for familiarization rhythm, $F(3, 136) = 0.68, p > 0.05$. The identity of the familiarization rhythm did not impact head turning in the test trials.

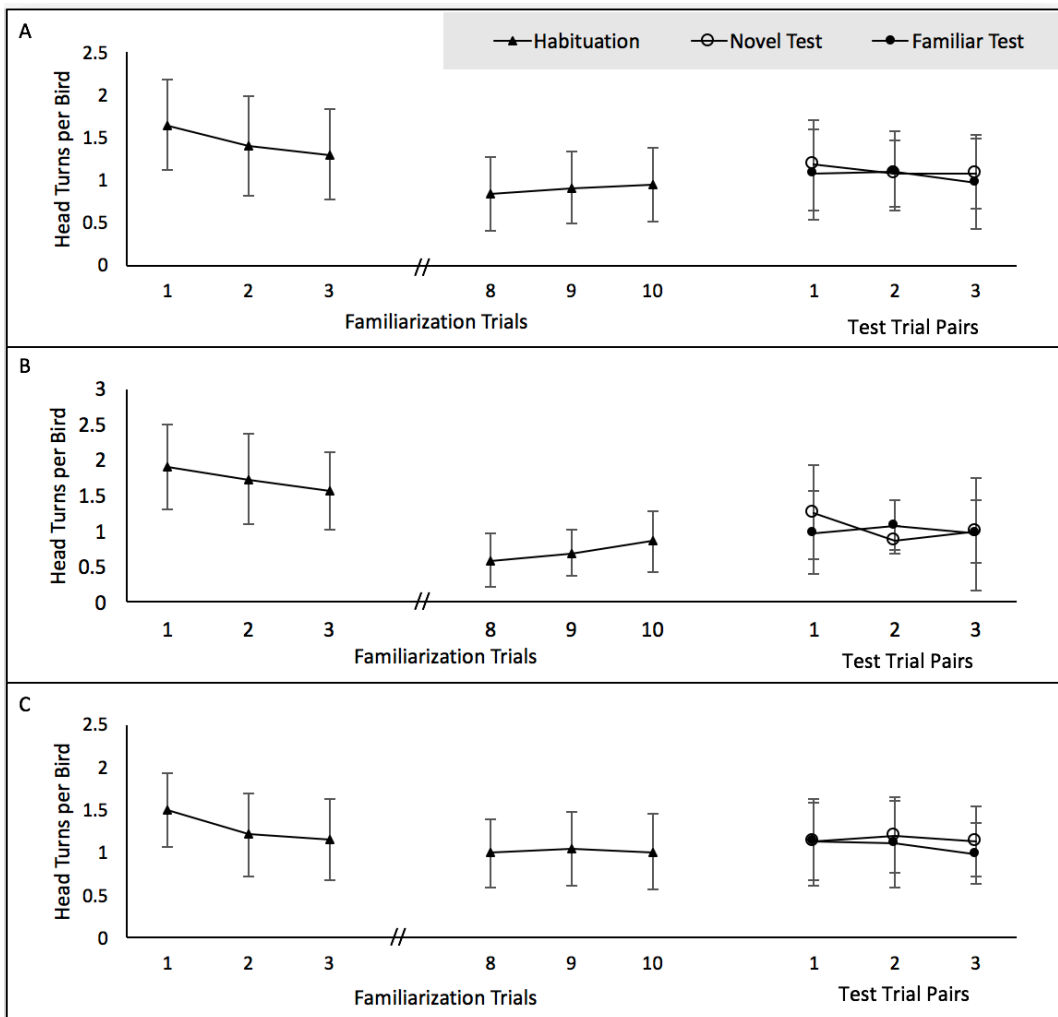


Figure 5. Head turns per bird for habituation and test trials in A) all twenty-four sessions, B) all nine sessions where the penguins met the habituation criterion and C) all fifteen sessions where penguins did not meet habituation criterion. Error bars mark the standard deviation of the mean.

4. CONCLUSIONS

This study was the first to explore auditory rhythm perception in penguins using a habituation-dishabituation paradigm. Analyses of African penguin ecstatic display songs suggest that there are rhythmic properties in penguin vocalizations (Favaro et al., 2015, Thumser & Ficken, 1996). Inter-individual differences in the rhythms of African penguin vocalizations may play a part in auditory kin recognition (Favaro et al., 2015). Additionally, penguin vocalizations that are used to communicate different scenarios, such as locating an individual penguin in a crowd or advertising territory occupation, have different rhythms and are emitted by penguins regularly (Favaro et al., 2014). However, none of the previous studies aimed to learn whether penguins perceived these differences in rhythm. The results of the current study provided no evidence for rhythm perception in African penguins. One possible conclusion to draw from these results is that penguins are unable to perceive differences in auditory rhythms. Alternatively, one could conclude that the present study did not reveal rhythm perception in penguins because of the limitations and constraints of the chosen method. The habituation-dishabituation method was selected for this study because it is a way to study auditory perception without extensive animal training (which can take months to years). However, there were still constraints. These constraints included a small number of test sessions as well as methodological restrictions associated with limitations placed on the study by the zoo. Because of time limitations, only 24 test sessions were conducted, and penguins only met habituation criterion in 9 of the 24 sessions. Also, because we were unable to separate penguins, penguins were tested in groups rather than testing them individually, and the groups of penguins were repeatedly exposed to each of the rhythmic stimuli used in the study, which is never done in infant habituation-dishabituation studies. In traditional habituation-dishabituation studies one infant is habituated to a stimulus and played a novel stimulus one time (Kavsek & Bornstien, 2010). This is also the case for some habituation-dishabituation studies with non-human animals (Fischer, 1998; Ramus et al., 2000; Svedsen et al., 2012).

Based on what is known about penguin vocalizations and their ecological functions, it is likely that future studies using a different methodology or test procedures may reveal that penguins can perceive rhythm. Because of the expanding body of research supporting rhythm perception throughout the animal kingdom, it is becoming more accepted as an adaptive, widespread perceptual ability. The benefits of rhythm perception seem to be important to animals in many elements of their lives. Rhythm perception allows for complex communication and synchronous behavior. Rhythm perception also enables animals to anticipate the timing of stimuli (whether they be auditory, visual or tactile) in their environments which ultimately increases species survival.

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