Pitch Perception in Chinchillas (Chinchilla laniger): Stimulus Generalization Using Rippled Noise

William P. Shofner
Indiana University

William A. Yost and William M. Whitmer
Loyola University Chicago

Rippled noises evoke the perception of pitch in human listeners. Infinitely iterated rippled noise (IIRN) is generated when wideband noise (WBN) is delayed, attenuated, and added to the original WBN through either a positive (+) or a negative (−) feedback loop. The pitch of IIRN[+] is matched to the reciprocal of the delay, whereas the pitch of IIRN[−] for the same delay is an octave lower. Chinchillas (Chinchilla laniger) were trained to discriminate IIRN[+] with a 4-ms delay from IIRN[+] with a 2-ms delay and then tested in a stimulus generalization paradigm with IIRN[+] at delays between 2 and 4 ms. Systematic gradients in behavioral response occurred along the dimension of delay, suggesting that a perceptual dimension corresponding to pitch exists for IIRN[+]. Behavioral responses to IIRN[−] test stimuli were more variable among chinchillas, suggesting that IIRN[−] did not evoke similar pitches relative to IIRN[+]. Systematic gradients in behavioral response were observed when IIRN[−] test stimuli were presented in the context of other IIRN[−] stimuli. Thus, other perceptual cues such as timbre may dominate the pitch cues when IIRN[−] test stimuli are presented in the context of IIRN[+] stimuli.

Keywords: chinchilla, pitch perception, rippled noise, stimulus generalization

A perception of pitch is evoked by many different complex sounds, including speech and music, and different complex sounds can produce the same pitch (Fastl & Stoll, 1979). There exist many different adjectives to describe the variety of pitch perceptions generated by the different types of complex sounds: spectral pitch is generated by simple tones; nonspectral pitch is generated by sinusoidal amplitude modulated noise; periodicity pitch is generated by harmonic complex tones composed of the low-frequency, resolved components; residue pitch is generated by harmonic complex tones composed of the high-frequency, unresolved components; repetition pitch is generated by rippled noise. Rippled noises are pseudoperiodic sounds; that is, the waveforms possess periodic temporal regularities, but these regularities are not repeated in a periodic manner. Consequently, rippled noises have become an important class of stimuli for studying the perception of pitch and have proved useful for testing models of pitch perception (Cohen, Grossberg, & Wyse, 1995; Meddis & Hewitt, 1991; Shamma & Klein, 2000; Yost, Patterson, & Sheft, 1996).

Rippled noises are generated when a time-delayed, attenuated version of wideband noise (WBN) is added to or subtracted from the original WBN. Consequently, the flat-spectrum input is converted into an output stimulus having spectral ripples at frequencies related to the delay. A variety of different delay-and-add networks can be used to generate rippled noise (see Yost, 1996). Figure 1 illustrates the network used for generating rippled noises for the present study, which uses a positive (+) or negative (−) feedback loop. Rippled noises generated from this type of network are known as infinitely iterated rippled noises (IIRNs) (Shofner & Yost, 1995), comb-filtered noises (Raatgever & Bilsen, 1992), or peaked rippled noises (Fastl, 1988). For convenience, the parameters of IIRN are described using the following notation: IIRN[+/−, T, dBattenu], where +/- indicates whether the feedback loop is positive or negative, T is the delay in milliseconds, and dBattenu is the attenuation of the delayed noise relative to the original, undelayed version of the noise. Thus, the example spectrum shown in Figure 1 for IIRN[+, 4 ms, −1 dB] is an IIRN generated through a positive feedback loop with a delay of 4 ms and a delayed noise attenuation of −1 dB.

The pitch perception evoked by the rippled noise is related to the delay. In general, the pitch of IIRN[+] is at a frequency corresponding to 1/T, whereas the pitch of IIRN[−] is at 1/(2T) (Raatgever & Bilsen, 1992; Yost, 1996); that is, the pitch of IIRN[−] is one octave lower than IIRN[+] of the same delay. The saliency or strength of the pitch perception is related to the amount of attenuation in the circuit; as more attenuation is added to the circuit, the resulting rippled noise evokes a stronger noise percept and a weaker pitch percept (e.g., Shofner & Selas, 2002). In the present study, the delay was varied, but the delayed-noise attenuation remained fixed. Thus, for the rippled noises in the present study, the perceptual dimension corresponding to pitch varied, but the perceptual dimension for pitch strength remained relatively constant.

Also shown in Figure 1 is an example autocorrelation function for the IIRN generated in the positive feedback loop. Positive correlations (i.e., peaks) occur in the autocorrelation function at...
integer multiples of the delay, and the peaks in the autocorrelation function are an indication of the amount of temporal regularity in the waveform. The first peak in the autocorrelation function is referred to as \( AC_{\text{peak1}} \). The time lag where \( AC_{\text{peak1}} \) is located is related to the perceived repetition pitch (see Yost, 1996), and in this example, the time lag of \( AC_{\text{peak1}} \) corresponds to the delay, \( T \). Note that for WBN, the autocorrelation function is flat, indicating that no temporal regularities exist in the waveform; consequently, WBN does not evoke a perception of pitch. Figure 2 shows the comparison of the temporal and spectral characteristics of IIRNs generated using positive and negative feedback loops. The top left-hand panel shows the autocorrelation function for IIRN generated in a positive feedback loop with a delay of 4 ms. Note that there are positive correlations (i.e., peaks) at integer multiples of the 4-ms delay and that \( AC_{\text{peak1}} \) occurs at 4 ms. The magnitude or height of \( AC_{\text{peak1}} \) is 0.825 in this example. In the spectrum, the first peak occurs at 250 Hz, and all successive peaks are separated by 250 Hz (see the top right-hand panel of Figure 2). In human listeners, this rippled noise evokes a salient pitch of 250 Hz. If a negative feedback loop is used to generate the IIRN with the same 4-ms delay, then the autocorrelation function shows alternating negative and positive correlations (i.e., nulls and peaks) with the
first null at the 4-ms delay and the first peak at 8 ms (middle left-hand panel of Figure 2). Thus, when a negative feedback loop is used, the resulting rippled noise has an ACpeak1 occurring at a time lag equal to twice the delay. In the spectrum, the first peak occurs at 125 Hz, and successive spectral peaks are separated by 250 Hz. In human listeners, this rippled noise evokes a salient pitch of 125 Hz, one octave below that for the positive condition. If a negative feedback loop is used and the delay is at 2 ms, then

Figure 2. Examples of the temporal and spectral characteristics of infinitely iterated rippled noises (IIRNs). Top: characteristics for IIRN [+ 4 ms, -1 dB]. Middle: characteristics for IIRN [-, 4 ms, -1 dB]. Bottom: characteristics for IIRN [-, 2 ms, -1 dB]. The left-hand columns show autocorrelation functions (temporal); arrows indicate the first peak in the autocorrelation function (ACpeak1). The right-hand columns show spectra; single arrows indicate the first spectral peak, which corresponds to 1/ACpeak1; horizontal double-headed arrows indicate the frequency difference between spectral peaks, which corresponds to 1/T, where T is the delay. Norm = normalized.
ACPeak1 occurs at a time lag of 4 ms in the autocorrelation function, and the first spectral peak is at 250 Hz with successive peaks separated by 500 Hz (see bottom panels of Figure 2). In human listeners, this rippled noise also evokes a salient pitch of 250 Hz. Although the rippled noises illustrated in the top and bottom panels both evoke matched pitches corresponding to 250 Hz, they can be discriminated easily from one another, presumably because the spectral differences give rise to timbre differences (e.g., Singh & Hirsh, 1992).

Many of the pitch studies in human listeners have used methods such as matching and scaling procedures in order to address issues concerned with a participant’s perception rather than with a participant’s sensory acuity as would be determined by measuring detection or discrimination thresholds. Although detection and discrimination thresholds can be measured in animals, it is not feasible to use matching or scaling procedures in animals. That is, subjective procedures such as pitch matching and magnitude estimation do not have a direct counterpart in animal behavioral experiments in the way that objective discrimination procedures do. However, stimulus generalization paradigms can be used to address perceptual questions in animals. In stimulus generalization paradigms, an animal is trained to respond to a specific training stimulus, and then responses are measured to probe or test stimuli that vary along one or more physical dimensions or stimulus features (Mallott & Mallott, 1970). Behavioral responses to test stimuli that are equal to responses to the specific training stimulus suggest a perceptual equivalence among the stimuli (Hulse, 1995). That is, perceptual equivalence occurs when the animal perceives there to be a common stimulus feature among the training and test stimuli. If a systematic gradient in behavioral response occurs as the stimulus dimension changes, then the animal orders the stimuli along the stimulus dimension. This ordering of stimuli along a physical dimension is known as a generalization gradient, and it presumably reflects the existence of a perceptual dimension corresponding to the physical dimension of the stimulus (Guttman, 1963). Thus, data from stimulus generalization paradigms can indicate what stimulus features control the behavioral response of the animal.

A perceptual dimension corresponding to tone frequency has been established in rats (Blackwell & Schlosberg, 1943), several species of birds (Cynx, 1993; Dooling, Brown, Park, Okanoya, & Soli, 1987; Jenkins & Harrison, 1960), and goldfish (Fay, 1992). Moreover, starlings (Cynx & Shapiro, 1986), cats (Heffner & Whitfield, 1976; Whitfield, 1980), and rhesus monkeys (Tomlinson & Schwarz, 1988) appear to have a percept corresponding to the missing fundamental frequency of a complex tone. However, the existence of a perceptual dimension corresponding to rippled noise delay has only been investigated in goldfish. Using a discrimination paradigm, Fay, Yost, and Coombs (1983) showed that the thresholds for goldfish are close to those of human listeners for discriminating rippled noises of different delays. However, when trained to detect a rippled noise of one delay and tested with rippled noises in a stimulus generalization paradigm, goldfish did not show a gradient in behavioral responses (Fay, 2005). In this latter experiment, Fay (2005) concluded that the lack of a generalization gradient in goldfish is because any pitch percept evoked by rippled noise is likely to be weaker than the noise percept evoked by rippled noise. Thus, whether a perceptual dimension corresponding to rippled noise delay exists in nonhuman vertebrates remains an open question.

Defining the perceptual characteristics of rippled noises in animals is an important conceptual link when making comparisons between the perception of repetition pitch in human listeners and the responses of single neurons to rippled noise obtained from animals (e.g., Shofner, 1999; Wiegrebe & Winter, 2001). Previous studies have shown that chinchillas discriminate IIRN from WBN using processes similar to those in human listeners (Shofner & Yost, 1995, 1997) and that chinchillas possess a perceptual dimension related to the periodicity strength of the IIRN (Shofner, Whitmer, & Yost, 2005). However, it is unknown whether a perceptual dimension related to rippled noise delay exists in the chinchilla. In the experiments reported in this article, we used stimulus generalization procedures to study the perceptual attributes of rippled noise delay in the chinchilla.

**General Method**

**Subjects**

Adult chinchillas (Chinchilla laniger) served as subjects in these experiments. All 5 chinchillas used in the present study had extensive experience in the behavioral paradigm and had served as subjects in previous studies measuring “pitch” strength (Shofner & Whitmer, 2006; Shofner et al., 2005). In these pitch-strength experiments, chinchillas discriminated IIRN+1 from a wideband, flat-spectrum noise. Chinchillas received food pellet rewards during behavioral testing, and their diets were supplemented with chinchilla chow to maintain their body weights at around 80% to 90% of normal weight. They received a raisin as a treat following each daily behavioral test session. Although chinchillas were food restricted, they had free access to water. They were housed individually in rabbit cages in a room in the animal care facility, and all chinchillas appeared in good health during the period when their data were being collected. Chinchillas were tested daily in a session that typically lasted 1 hr.

**Acoustic Stimuli**

Stimuli consisted of IIRNs as generated by the circuit illustrated in Figure 1. The input WBN to the circuit was generated with a Model 132 VCG/Noise generator (WaveTek, San Diego, CA) in which the parameters were set to yield a pseudorandom noise that repeated itself every 6.55 s and had a bandwidth of 10 kHz. This noise was then divided into two channels and fed into a digital delay line (Model PD 860 Precision Delay Line; Eventide, Little Ferry, NJ). IIRN+[+] was generated when the delayed version of the WBN was added to the original WBN through a positive feedback loop, whereas IIRN[−] was generated using a negative feedback loop. The delay line uses a sampling rate of 62.5 kHz. The outputs of the two delay line channels were low-pass filtered at a cutoff frequency of 15 kHz (FT5 module; Tucker-Davis Technologies [TDT], Alachua, FL) and summed together (TDT SM3 module). In this study, the amount of attenuation of the delayed noise was fixed at −1 dB for all IIRNs using a program- mable attenuator (TDT PA4 module). For each IIRN generated, 5 s of the waveform was sampled at 50 kHz and stored as a stimulus file. For each block of 40 trials during behavioral testing (see
below), a random 500-ms sample of each IIRN was extracted from the 5-s stimulus files. Each 500-ms IIRN stimulus was shaped with 10-ms rise–fall times.

Stimulus presentation and data acquisition were under the control of a Gateway computer system and TDT System II modules. Stimuli were played through a digital-to-analogue converter (TDT DD1 module) at conversion rate of 50 kHz and low-pass filtered at 15 kHz. The output of the low-pass filter was amplified, attenuated (TDT PA4 module), and played through a loudspeaker (Radio Shack, Fort Worth, TX). The overall sound pressure level (SPL) of the IIRN stimuli was determined by placing a condenser microphone (Ivie 1133) at the approximate position of a chinchilla’s head and measuring the A-weighted SPL with a sound level meter (IE-30-A Audio Spectrum Analyzer; Ivie Technologies, Lehi, UT).

In this study, the SPL was fixed at 73 dB for all stimuli.

**Behavioral Procedure**

Chinchillas were placed into a cage (40.6 × 30.5 × 25.4 cm); they were not restrained in any way but were free to roam around the cage. The cage was placed in a single-walled sound-attenuating animal test chamber (Industrial Acoustics) that was lined with acoustic foam. A pellet dispenser was located at one end of the cage with a reward chute attached to a response lever. The loudspeaker was placed next to the pellet dispenser approximately 30° to the right of center at an approximate distance of 6 in. (about 15.2 cm) in front of the chinchilla. The behavioral procedure was based on an operant conditioning paradigm and has been used previously to study the perception of periodicity strength in chinchillas (Shofner, 2002; Shofner & Whitmer, 2006; Shofner et al., 2005). It was similar to a procedure used by Ohlemiller, Jones, Heidbreder, Clark, and Miller (1999) to study categorical perception of consonant–vowel syllables in chinchillas.

Figure 3 illustrates the behavioral procedure. A standard stimulus was presented continually in 500-ms bursts at a rate of once per second, regardless of whether or not a trial was initiated. Chinchillas were trained to discriminate a signal stimulus from the standard stimulus. A trial was initiated when the chinchilla pressed down on the response lever. The lever must be depressed for a specified duration of time that is referred to as the hold time. After the lever was depressed, the standard stimulus was presented for one to eight bursts. The number of additional bursts was determined for each trial from a rectangular probability distribution and resulted in a random hold time of 1.15 to 8.15 s. If the chinchilla released the lever before the hold time expired, then the countdown of the hold time was halted; that hold time began again with the next lever press. If the chinchilla depressed the lever for the duration of the hold time, then one of four stimuli were presented for that trial (see Figure 3). The response window was coincident with the duration of the trial, which consisted of two 500-ms bursts of a selected stimulus. The response window, however, actually began 150 ms after the onset of the first burst and lasted until the onset of the next burst of the continual standard stimulus. A release of the lever during the response window was considered to be a positive response, whereas continuing to depress the lever for the duration of the response window was considered to be a negative response.

A signal trial consisted of two bursts of the signal stimulus. If the chinchilla released the lever during the response window of a signal trial, then this positive response was treated as a hit. A negative response during a signal trial was then treated as a miss. A blank trial consisted of two additional bursts of the standard stimulus. If the chinchilla released the lever during the response window of a blank trial, then this positive response was treated as a false alarm. A negative response during a blank trial was treated as a correct rejection. Hits and correct rejections were correct responses and were rewarded with food pellets, whereas misses and false alarms were incorrect responses and, as such, were not rewarded with food pellets. That is, positive and negative responses during signal or blank trials were treated as objective responses. A test trial consisted of two bursts of either of two different test or probe stimuli. Chinchillas did not receive food pellet rewards for responses to test stimuli, regardless of whether the behavioral response was positive or negative. Behavioral responses to the test stimuli were considered to be neither correct nor incorrect but rather to be subjective responses.

Chinchillas were trained and tested in blocks consisting of 40 trials. During periods of training, no test stimuli were presented, and a block of 40 trials consisted of 32 signal trials and 8 standard trials. During testing sessions, test stimuli were presented infrequently in the block of trials such that in each block, 60% of the trials were signal trials (24 of 40 trials), 20% were blank trials (8 of 40 trials), 10% were Test Stimulus 1 trials (4 of 40 trials), and 10% were Test Stimulus 2 trials (4 of 40 trials). Because chinchillas only received food pellets for correct responses during signal and blank trials, chinchillas could potentially be rewarded for 80%
of the total trials (i.e., 24 signal + 8 blank trials). Behavioral responses were collected for a minimum of 50 blocks (totaling 2,000 trials), which resulted in a minimum of responses to 200 trials for each of the two test stimuli presented. Chinchillas typically completed 2 to 8 blocks per day.

Experiment 1: IIRN[+] Tests in the Context of IIRN[+] Comparisons

Method

The purpose of this first experiment was to determine whether chinchillas possess a perceptual dimension corresponding to pitch that was related to the delay of IIRN[+]. In this experiment, the standard stimulus was IIRN[+, 2 ms, −1 dB] and the signal stimulus was IIRN[+, 4 ms, −1 dB]. In human listeners, this standard stimulus has a repetition pitch of 500 Hz, whereas the signal stimulus has a repetition pitch of 250 Hz. Because the chinchillas had previous experience in the behavioral paradigm, it was only necessary to train the chinchillas to discriminate the signal stimulus from the standard stimulus. Prior to testing, the chinchillas were trained daily for a period of 1 week. Chinchillas easily obtained a 90% hit rate within this training period. The test stimuli used in this experiment consisted of IIRN[+] having delays (Ts) of 2.22, 2.50, 2.86, and 3.33 ms. Note that for IIRN[+], ACpeak1 is equal to the delay of the rippled noise and the corresponding repetition pitches will occur at 1/ACpeak1. For these test stimuli, the reciprocals of ACpeak1 correspond to 450, 400, 350, and 300 Hz, respectively. A systematic gradient in behavioral responses along the dimension of ACpeak1 (i.e., T) would be consistent with the existence of a perceptual dimension. This perceptual dimension corresponds to repetition pitch in human listeners.

Results

Figure 4 shows the behavioral responses obtained from 5 chinchillas when trained to discriminate IIRN[+, 4 ms, −1 dB] from IIRN[+, 2 ms, −1 dB] and tested with IIRNs having Ts between 2 and 4 ms. The x-axis shows the time lag of ACpeak1 in milliseconds, which again for IIRN[+] corresponds to T. Behavioral response is shown as the percentage of positive responses, which is the percentage of trials on which the chinchilla released the lever during the response window for each particular stimulus. Figure 4 shows that when IIRN[+, 4 ms, −1 dB] was presented during the response window (i.e., as ACpeak1 = 4 ms), the percentage of positive responses was large. That is, there was a large number of lever releases when the signal stimulus, IIRN[+, 4 ms, −1 dB], was presented. In contrast, when IIRN[+, 2 ms, −1 dB] was presented during the response window (i.e., ACpeak1 = 2 ms), then the percentage of positive responses was small. That is, there were few lever releases when the standard stimulus, IIRN[+, 2 ms, −1 dB], was presented. Moreover, when the test stimuli were presented and there was an increase in the time lag of ACpeak1 from 2 to 4 ms, there was a corresponding systematic increase in behavioral response. That is, there was a systematic increase in the number of lever releases during the response window as ACpeak1 of the IIRN stimulus increased from 2 to 4 ms. Figure 5A shows the average percentage of positive responses obtained from the 5 chinchillas as a function of the repetition pitch, 1/ACpeak1. The thin line is the best fitting regression line through the average data. This figure shows that over this range of delays, which corresponds to an octave change in 1/ACpeak1 from 500 to 250 Hz, the average behavioral response can be predicted by a linear function on a semilog scale.

Experiment 2: IIRN[−] Tests in the Context of IIRN[+] Comparisons

Method

The purpose of this experiment was to determine whether IIRN[−] evokes a perception corresponding to pitch that is an octave lower than the corresponding IIRN[+]. In this experiment, the standard stimulus was again IIRN[+, 2 ms, −1 dB] and the signal stimulus was IIRN[+, 4 ms, −1 dB]. Because the chinchillas were already trained to make this discrimination for Experiment 1, no additional training was necessary. The test stimuli used in this experiment consisted of IIRN[−] having delays (Ts) of 1.0, 1.25, 1.67, and 2.0 ms. Note that for these IIRN[−], ACpeak1 now occurs at twice the delay (i.e., at 2T) of the rippled noise. The corresponding repetition pitches of 1/ACpeak1 are now at 1/(2T). For example, ACpeak1 for the IIRN[−, 2 ms, −1 dB] test stimulus will occur at the same time lag as ACpeak1 for the IIRN[+, 4 ms, −1 dB] signal stimulus (compare the top and bottom panels in Figure 2). Thus, for these IIRN[−] test stimuli, the reciprocals of ACpeak1 also correspond to 500, 450, 400, 350, and 250 Hz as in Experiment 1 using only IIRN[+]. A systematic gradient in behavioral responses along the dimension of ACpeak1 (i.e., 2T) would be consistent with the existence of a perceptual dimension corresponding to repetition pitch.

Results

Figure 6 shows the behavioral responses to the IIRN[−] test stimuli in the context of using IIRN[+] as the standard and signal stimuli. As a point of reference, each individual generalization gradient obtained using IIRN[+] stimuli in Experiment 1 is shown.
Experiment 3: IIRN[−] Tests in the Context of IIRN[+] Comparisons

Method

The lack of a systematic gradient in behavioral responses for IIRN[−] shown in Figure 6 could reflect an absence of a pitch percept evoked by IIRN[−] stimuli (see the Discussion section). That is, perhaps in the chinchilla, IIRN[−] stimuli do not evoke a perceptual dimension corresponding to repetition pitch the way that IIRN[+] stimuli do (i.e., Figure 4). Alternatively, it is possible that IIRN[−] stimuli do evoke a perceptual dimension corresponding to pitch, but the spectral differences between IIRN[−] and IIRN[+] stimuli evoke a perceptual dimension corresponding to timbre that dominates any pitch percept. In order to test this, we obtained generalization gradients in which IIRN[−] with Ts of 1.11, 1.25, 1.43, and 1.67 ms. For Chinchillas 16 and 29, no training was necessary as the chinchillas achieved hit rates of 90% on the 1st day; Chinchillas 40 and 41 were given 3 weeks and 1 week of training, respectively, before testing began.

Results

Unlike the responses observed in Figure 6 in which IIRN[−] stimuli were tested in the context of IIRN[+] standard and signal stimuli, Figure 7 shows the responses to IIRN[−] test stimuli obtained in the context of IIRN[−] standard and signal stimuli. Three of the 4 chinchillas tested (Chinchillas 16, 40, and 41) appeared to show a systematic increase in percentage of positive responses as ACpeak1 of the IIRN[−] stimuli increased from 2 to 4 ms. Comparison of the behavioral responses to IIRN[−] with those to IIRN[+] (solid circles vs. open circles in Figure 7) indicates that the generalization gradients are similar for the two sets of stimuli. One chinchilla (Chinchilla 29) gave a generalization gradient for IIRN[−] that was not as systematic and deviated more from the IIRN[+] gradient.

A comparison of the behavioral responses as a function of repetition pitch is shown in Figure 5 for IIRNs generated using the positive and negative feedback loops. Repetition pitch is defined as 1/ACpeak1 in hertz. These functions show the mean positive responses and the 95% confidence intervals. As the repetition pitch of the IIRN decreased from 250 Hz, there was a systematic decrease in the percentage of positive responses for both IIRN[+] (see Figure 5A) and IIRN[−] (see Figure 5B). The data can be well fit with linear functions. The slope of the best fitting IIRN[+] regression line is −297, and the y-intercept is 805 (Figure 5A); the slope of the best fitting IIRN[−] regression line is −315, and the y-intercept is 845 (Figure 5B). The r² values for the IIRN[+] and IIRN[−] regression lines are .985 and .970, respectively.
Discussion

Behavioral responses were measured from chinchillas using a stimulus generalization paradigm to IIRNs that varied in delay. Stimulus generalization paradigms are designed to address questions more concerned with measuring perception in animals rather than with measuring sensory acuity as in detection and discrimination paradigms. In a stimulus generalization paradigm, animals are trained to discriminate a specific training or signal stimulus from a comparison or standard stimulus. Behavioral responses are then measured for probe or test stimuli that vary systematically along one or more stimulus dimensions (Mallott & Mallott, 1970).

Systematic changes in behavioral responses along a stimulus dimension are referred to as stimulus generalization gradients and are interpreted to be a reflection of the psychological or perceptual dimension of the stimulus (Guttman, 1963). Behavioral responses to test stimuli that are similar in magnitude to responses to the signal stimulus are interpreted to indicate a perceptual equivalence among the stimuli (Hulse, 1995); that is, from a functional viewpoint, these stimuli contain a feature that makes the animal perceive the stimuli to be equivalent or similar.

In the present study, the stimulus dimension in question is the delay of the rippled noise, or more specifically ACpeak1. The

Figure 6. Percentage of positive responses as a function of the first peak in the autocorrelation function (ACpeak1) for infinitely iterated rippled noise (IIRN) test stimuli obtained from 5 chinchillas (Cs). The standard stimulus was IIRN[+, 2 ms, -1 dB], and the signal stimulus was IIRN[+, 4 ms, -1 dB]. Open circles with dotted line are generalization gradients obtained from Experiment 1 and shown in Figure 4. Solid circles show the percentage of positive responses to the IIRN[+, 2 ms, -1 dB] standard and the IIRN[+, 4 ms, -1 dB] signal when tested with IIRN[-] stimuli. Percentage of positive responses to IIRN[-] are shown in the gray-shaded squares. The vertical double-headed arrows show the difference between the responses to the IIRN[+, 4 ms, -1 dB] signal stimulus and the IIRN[+, 2 ms, -1 dB] test stimulus. Both of these have ACpeak1s of 4 ms. The percentages indicate the amount that the responses to IIRN[+, 4 ms, -1 dB] decreased relative to that for the IIRN[+, 4 ms, -1 dB].
Stimulus Generalization

![Graphs showing stimulus generalization](image)

**Figure 7.** Comparison of behavioral responses for infinitely iterated rippled noise (IIRN)[+] and IIRN[−] stimuli obtained from 4 chinchillas (Cs) in the stimulus generalization procedure. Each panel shows generalization gradients as the percentage of positive responses as a function of the first peak in the autocorrelation function (ACpeak1). Solid circles with solid lines show generalization gradients obtained from when the standard stimulus was IIRN[−, 1 ms, −1 dB] and the signal stimulus was IIRN[−, 2 ms, −1 dB]; test stimuli were IIRN[−] having delays (Ts) of 1.11, 1.25, 1.43, and 1.67 ms. Open circles with dotted lines show gradients obtained from Experiment 1 when the standard stimulus was IIRN[+, 2 ms, −1 dB] and the signal stimulus was IIRN[+, 4 ms, −1 dB]; test stimuli were IIRN[+] having Ts of 2.22, 2.5, 2.86, and 3.33 ms. Note that C41 developed a prolapsed bowel before collection of the data was completed for two of the IIRN[−] test stimuli with Ts of 1.11 and 1.43 ms (i.e., ACpeak1s of 2.22 and 2.86 ms, respectively). Consequently, this chinchilla was removed from the remainder of the study.

repetition pitch is directly related to the time lag of ACpeak1 in human listeners (Yost, 1996). Chinchillas were trained to discriminate an IIRN[+] signal with an ACpeak1 at 4 ms from an IIRN[+] standard with an ACpeak1 at 2 ms. In human listeners, this represents an octave change in pitch from 500 Hz (standard) to 250 Hz (signal). Chinchillas show monotonic changes in behavioral response as ACpeak1 of IIRN[+] changes from 2 to 4 ms (Experiment 1). That is, chinchillas systematically order these IIRN[+] stimuli along a physical dimension of ACpeak1. Figure 5A shows that the behavioral response of the chinchilla as a function of the reciprocal of ACpeak1 (i.e., frequency in hertz) is represented well by a straight line when plotted in linear-log coordinates. The generalization gradient in the chinchilla is consistent with the existence of a perceptual dimension that corresponds to rippled noise pitch (i.e., repetition pitch). That is, the repetition pitch scale over the octave range of 250 to 500 Hz for chinchillas is a linear function on a linear-log coordinate system. It is interesting to note that the shape of the pure tone pitch scale for humans and budgerigars (Dooling et al., 1987) and in starlings (Cynx, 1993) over a narrow frequency range on the order of one octave is also linear in a linear-log coordinate system. Nonlinear pitch scales are obtained when the frequency range is several octaves wide (Blackwell & Schlosberg, 1943; Dooling et al., 1987).

Although rippled noise processing has been examined in birds (Amagai, Dooling, Shamma, Kidd, & Lohr, 1999) and mammals (e.g., Shofner & Yost, 1995; Shofner et al., 2005), these studies have not been concerned with pitch processing per se but rather...
have addressed issues regarding periodicity strength of rippled noises. That is, the discriminations were between a rippled noise and a wideband, flat-spectrum noise (i.e., coloration discrimination) rather than between rippled noises of different delays (i.e., pitch discrimination). There is one other study in which the existence of a perceptual dimension corresponding to rippled noise delay was addressed. In goldfish, Fay (2005) examined the existence of a pitchlike dimension for rippled noise stimuli using stimulus generalization. This study showed that goldfish generalized to all rippled noise stimuli when trained to detect a rippled noise signal having a specific delay. That is, goldfish responded to all test rippled noises with the same probability as their response to the signal rippled noise and, consequently, did not produce a generalization gradient. The lack of a generalization gradient is suggestive that a perceptual dimension corresponding to rippled noise delay is weak or nonexistent in goldfish (Fay, 2005). Nevertheless, goldfish do appear to possess pitchlike perceptual dimensions corresponding to tone frequency (Fay, 1992) and the fundamental frequency of complex tones (Fay, 2005). The noise percept of the rippled noise appears to overwhelm any pitch percept evoked by the rippled noise (Fay, 2005). The stimulus generalization gradients along the physical dimension of ACpeak1 obtained in the present study are the first reported data indicating that a perceptual dimension corresponding to rippled noise delay exists in nonhuman vertebrates.

When chinchillas were trained using IIRN[+] stimuli and tested using IIRN[−] stimuli (Experiment 2), monotonic changes in behavioral response were not observed as ACpeak1 changed from 2 to 4 ms. That is, chinchillas did not order IIRN[−] test stimuli systematically along the physical dimension of ACpeak1. The lack of a generalization gradient could be interpreted as a lack of a pitchlike perception for IIRN[−] corresponding to the reciprocal of ACpeak1. That is, IIRN[−] stimuli may not be perceptually equivalent to IIRN[+] stimuli having the same values of ACpeak1 and, thus, do not evoke a pitchlike perception in chinchillas. What might control the behavioral response of the chinchilla in this experiment if it is not the location of ACpeak1? First, the magnitude of ACpeak1 could affect the behavioral response, and second, the spectral differences (see Figure 2) could affect the behavioral response.

It has previously been shown that the magnitude of ACpeak1 of rippled noise is related to the perceptual dimension corresponding to pitch strength in chinchillas (Shofner et al., 2005) as well as in humans (Shofner & Selas, 2002). However, pitch strength seems to be an unlikely cue for controlling the behavioral responses of the chinchilla in the present study for two reasons. First, the magnitude of ACpeak1 for the comparison stimuli (i.e., IIRN[+, 4 ms, −1 dB] and IIRN[+, 2 ms, −1 dB]) are both around a value of 0.8 (see Figure 2 for IIRN[+, 4 ms, −1 dB] example). Thus, if the discrimination between this standard stimulus and this signal stimulus was solely based on pitch strength, then these two stimuli could not be discriminated and the behavioral responses would be equal. Second, as can be observed in Figure 6 (solid circles), the behavioral responses obtained to the standard were low, whereas the behavioral responses obtained to the signal were high, suggesting that these rippled noises are easily discriminated by the chinchilla. The magnitudes of ACpeak1 for the IIRN[−] test stimuli ranged from 0.614 to 0.720 with a median value of 0.631. This median value is close to the magnitude of ACpeak1 for IIRN[+].

A perceptual dimension corresponding to timbre could have an influence on the behavioral responses to IIRN[−] test stimuli in the context of IIRN[+] comparison stimuli. For example, consider IIRN[+, 4 ms, −1 dB] and IIRN[−, 2 ms, −1 dB] as illustrated in the top and bottom panels of Figure 2. Both stimuli share common features, namely, an ACpeak1 corresponding to a time lag of 4 ms and a first spectral peak located at 250 Hz. However, there are considerable spectral differences between the two stimuli. IIRN[+, 4 ms, −1 dB] has spectral peaks at all integer multiples of 250 Hz, whereas IIRN[−, 2 ms, −1 dB] has spectral peaks only at the odd integer multiples of 250 Hz. For complex sounds that are equal in loudness and pitch, differences in timbre can occur when there are spectral differences. Singh and Hirsh (1992) showed that for human listeners, timbre is influenced primarily by spectral locus, whereas pitch is influenced primarily by the fundamental frequency. Thus, the spectral differences described above for IIRN[+] and IIRN[−] stimuli could evoke a perception corresponding to timbre in the chinchilla. In the present study, the lack of a generalization gradient to IIRN[−] stimuli in the context of IIRN[+] comparison stimuli may reflect a perception corresponding to timbre. That is, the behavioral response of the chinchilla to IIRN[−] in the context of IIRN[+] may have been under the control of spectral differences between IIRNs rather than temporal similarities between IIRNs.

To gain some insight into whether the behavioral responses of chinchillas to IIRN[−] in the context of IIRN[+] stimuli were controlled by pitchlike cues or timbralike cues, we tested chinchillas with IIRN[−] stimuli using IIRN[+] standard and signal stimuli. That is, responses to IIRN[−] test stimuli were now measured in the context of IIRN[−] comparison stimuli. Thus, in this experiment, pitch differences between the comparison and test stimuli should remain, whereas timbre differences between comparison and test stimuli should be eliminated or reduced. That is, in Experiment 3 there were systematic differences in the location of ACpeak1 and all stimuli had spectral peaks only at odd integer multiples of 1/(2T).

When chinchillas were trained using IIRN[−] comparison stimuli and tested with IIRN[−] stimuli (Experiment 3), monotonic changes in behavioral response were now observed as ACpeak1 changed from 2 to 4 ms. That is, most chinchillas showed monotonic changes in behavioral response as ACpeak1 of IIRN[+] changed from 2 to 4 ms, indicating that chinchillas systematically order these IIRN[−] stimuli along a physical dimension of ACpeak1. One chinchilla (Chinchilla 29) did show a generalization gradient that was not as orderly as that obtained for IIRN[+] stimuli with a delayed noise attenuation of −3 dB (see Figure 2 of Shofner, 2002). When IIRN[+] was used as the signal stimulus and delayed noise attenuation was varied from −1 dB to −3 dB, the behavioral responses decreased from greater than or equal to 90% to around 50% to 60% (see Shofner et al., 2005). If the behavioral responses in the present experiment were being controlled solely by pitch strength, then it would be expected that behavioral responses would be around 50% for all IIRN[−] test stimuli. Figure 6 clearly shows that this is not the case; behavioral responses to IIRN[−] test stimuli in the context of IIRN[+] comparison stimuli do not appear to be controlled by the perceptual dimension corresponding to pitch strength.
stimuli. For most chinchillas, however, the generalization gradients for IIRN− were similar to those for IIRN+[+] (see Figure 7). The IIRN− generalization gradient in the chinchilla is consistent with the existence of a perceptual dimension that also corresponds to rippled noise pitch. Figure 5 shows that the behavioral response of the chinchilla as a function of the reciprocal of ACpeak1 (i.e., frequency in hertz) is represented by a straight line when plotted in linear-log coordinates for IIRN− stimuli as well as IIRN+[+] stimuli. Comparison of the two regression lines suggests that the perceptual dimension corresponding to a repetition pitch scale over the octave range of 250 to 500 Hz for chinchillas is similar for IIRN− and IIRN+[+] stimuli.

The systematic ordering of IIRN− test stimuli along a physical dimension of ACpeak1 in the context of IIRN− comparison stimuli suggests that IIRN− stimuli do indeed evoke a pitchlike perception in chinchillas. However, when IIRN− is placed in the context of IIRN+[+] stimuli as in Experiment 2, the perceptual dimension that corresponds to repetition pitch appears to be dominated by the perceptual dimension corresponding to timbre. Thus, in the context of IIRN+[+] comparison stimuli, the behavioral response of chinchillas to IIRN− is controlled by timbre cues rather than pitch cues. The dominance of timbre cues over pitch cues in this context has also been observed in other studies. For example, when goldfish are trained to respond to a pure tone, they do not generalize to any IIRN+[+] test stimuli, even to those rippled noises that would evoke the same pitch as the tone in human listeners (Fay, 2005). That is, IIRN+[+] stimuli are not perceptually equivalent to tones. Presumably, in the context of pure tones, IIRN+[+] test stimuli evoke more of a noise percept than a pitch percept in goldfish, and consequently, the behavioral responses of the goldfish to IIRN+[+] test stimuli are controlled by timbrelike cues rather than pitchlike cues. In human listeners, interactions between pitch and timbre can occur such that the timbre of a sound can have an influence on the perceived pitch of the sound (e.g., Singh & Hirsh, 1992; Warrier & Zatorre, 2002).

The results presented in this article indicate that a perceptual dimension corresponding to repetition pitch exists in chinchillas. A change in rippled noise delay has an effect on the behavioral response of the chinchilla, and, more important, the generalization gradient changes systematically as delay changes. A change in the rippled noise delay evokes a change in repetition pitch in human listeners. If a generalization gradient reflects the existence of a perceptual dimension corresponding to the physical dimension of the stimulus as argued by Guttman (1963), then a change in the delay of rippled noise also gives rise to a corresponding perceptual dimension in chinchillas.

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Received September 22, 2006
Revision received May 22, 2007
Accepted May 24, 2007

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