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Studies of Binaural Detection in the Rabbit (*Oryctolagus cuniculus*) With Pavlovian Conditioning

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A Pavlovian conditioned eyeblink response in rabbits (*Oryctolagus cuniculus*) was used to study psychoacoustical phenomena previously demonstrated in human listeners and other animals. This article contains the results of a tone-in-noise detection study to examine 2 psychoacoustical phenomena in rabbit and in human listeners: (a) the binaural masking level difference (BMLD) and (b) differential performance across reproducible noise masker waveforms. The rabbits demonstrated a BMLD comparable in size to other species. Significant differences in performance across reproducible noise masker waveforms were seen in the rabbits. This performance was compared with the performance of human listeners using the same set of waveforms.

Binaural cues are important for localization of sounds and for the detection and discrimination of signals in noisy environments. These problems can be studied at two levels: the average performance across many trials and performance on individual stimuli (Gilkey, Robinson, & Hanna, 1985; Green, 1964; Isabelle, 1995). Green (1964) introduced the expressions *molar* to describe average performance across waveforms and *molecular* to describe performance on individual trials. To examine the psychoacoustics of both average performance and performance on individual stimuli, a binaural psychoacoustical task was developed for the rabbit, an animal that has a long history of use in Pavlovian conditioning experiments (Gormezano, Kehoe, & Marshall, 1983). In this psychoacoustical task, two binaural phenomena were studied: (a) binaural unmasking, or the binaural masking level difference (BMLD) associated with detection of a tone in a noise masker, and (b) differential performance in the tone-detection task across individual reproducible noise maskers.

Most psychoacoustical studies involving noise maskers have used random noise samples or continuous random noise. However, it is possible to repeat a single digitally stored noise sample, or a set of stored noises. These stored and repeated noise samples are referred to as *reproducible noises.* The effects of individual reproducible noise maskers on performance in a tone-detection task have been investigated for human listeners since the 1960s (reviewed in Gilkey & Robinson, 1986). Gilkey et al. (1985) and Isabelle and Colburn (1991) used several different reproducible noise samples as a means of revisiting Green's (1964) attempts at modeling psychophysical performance for individual noise samples. Current models for binaural hearing that can explain the general phenomenon of the BMLD break down in the attempt to predict responses in the presence of individual reproducible noises (Isabelle, 1995).

The BMLD has been studied extensively in humans (reviewed by Bernstein, Trahiotis, & Hyde, 1998; Durlach & Colburn, 1978) and in other species, such as the cat (Cranford, 1975; Geesa & Langford, 1976; Hoppe & Langford, 1974; Wakeford & Robinson, 1974), ferret (Hine, Martin, & Moore, 1994), and budgerigar (Dent, Larsen, & Dooling, 1997). Differences across reproducible noise maskers have been studied in humans (Gilkey et al., 1985; Isabelle & Colburn, 1991; Siegel & Colburn, 1989) but not in other species. In this article, we describe the results of rabbit behavioral experiments with binaural, reproducible stimuli (Experiment 1). In addition, to confirm that the stimuli used in Experiment 1 resulted in the same effects as stimuli typically used in human experiments, we present a limited set of results from human listeners who completed experiments with the same set of stimuli as the rabbits (Experiment 2).

In the present experiments, we found the BMLD by comparing the detection threshold of identical tones to the two ears (the N_0S_0 condition) with the threshold of tones that are 180° out of phase (the N_0S_π condition) in the presence of a masking noise. The noise masker (N_0) waveform was the same in both ears for both cases. It has been shown, in humans and in other species, that the N_0S_π condition results in tone thresholds that are significantly lower than in the N_0S_0 condition, presumably because of the presence of binaural differences in the N_0S_π stimulus condition. For example, the BMLD in humans is approximately 12 dB when a 500-Hz tone

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is presented with a wideband noise masker (Durlach & Colburn, 1978). Other configurations of masker and signal phase have also been shown to result in binaural unmasking; however, the N_0S_0 and N_0S_π configurations were chosen for this experiment because they were studied in the previous experiments that focused on differential performance across reproducible noise samples (e.g., Gilkey et al., 1985; Isabelle & Colburn, 1991; Siegel & Colburn, 1989).

The threshold difference is consistent with the hypothesis that the listener can detect the N_0S_π signal as a decorrelation between the waveforms to the two ears (Colburn, 1977). The decorrelation allows detection at lower tone levels than when the completely correlated N_0S_0 signal is presented. A correlated, binaural noise (N_0) results in a large BMLD because the noise provides a baseline against which changes in binaural correlation can be detected. In contrast, the threshold difference between S_0 and S_π tones without noise maskers is less than 1 dB, and even this small difference can be explained by a model that includes masking provided by the internal noise of the listener (Diercks & Jeffress, 1962).

Previous studies in humans have shown that tone detection is also dependent on the exact reproducible noise masker (Gilkey et al., 1985; Isabelle & Colburn, 1991; Siegel & Colburn, 1989). Furthermore, this dependence varies to a certain extent between listeners; that is, a given reproducible noise masker may result in enhanced tone detectability for one listener and poor detectability for another listener.

Another feature of these noises is that some of the samples consistently sound as if they contain a tone when presented alone, causing listeners to consistently respond "yes, a tone was present" on noise-alone presentations. The noises that cause "yes" responses also differ to a certain extent across listeners. Studies with several reproducible noise maskers allow the investigation of details of the spectral and temporal properties of noises relative to their effectiveness as maskers. Noises that consistently elicit "yes" responses when no tone is present can also be studied to determine aspects of spectral and temporal properties that are associated with incorrect "yes" responses. As these incorrect "yes" responses may be influenced by the context, or the binaural condition being tested, these responses are always analyzed separately. Thus, these results are given an N_0S_0 or N_0S_π designation, which refers to the context in which these responses were made and not to the signal conditions themselves.

Although models have been developed that can explain the phenomenon of the BMLD when it is reported as an average across noises, these models fail when the phenomenon of differential performance across individual reproducible noises is examined. These binaural models fall into two categories, examined by Domnitz and Colburn (1976): those based on interaural amplitude and/or phase differences and those based on interaural correlation. Using an analysis of the stimulus spectra, Gilkey and Robinson (1986) found that a model based on a set of narrowband filters tuned near the frequency of the tone, each followed by a halfwave rectifier and an integrator, could successfully explain 40% to 70% of the variance of four listeners detecting tones in reproducible, diotic (N_0S_0), wideband noises. However, neither class of binaural model succeeded in predicting the performance of human listeners on an N_0S_π tone-detection task in the presence of reproducible, narrowband noises (Isabelle, 1995). This failure indicates that current models of binaural detection are too general to describe binaural processing on the level of individual reproducible noises. The most promising models studied by Isabelle (1995) were those that incorporated physiological models of the auditory periphery.

The long-term goals of studying the responses across reproducible noises include testing hypotheses that specific stimulus features in the reproducible noises correspond to performance differences and identifying auditory-processing strategies that may differ from subject to subject. In the current study, general features of the data were examined for correlations in performance across different stimulus conditions and subjects. Specifically, the correlations between correct responses to tone-plus-noise trials and incorrect responses to noise-alone trials, between the N_0S_0 responses and the N_0S_π responses, and among the responses of different listeners to the same stimuli were investigated across reproducible noises. In this way, the effect of specific aspects of the stimuli on responses to individual reproducible noises could be investigated. The long-term goal of this project is to study both the behavior and the physiology of BMLD and reproducible noise phenomena in the same subject. Physiological and behavioral responses to the same stimuli in the same subject should allow determination of specific stimulus properties that result in these responses, and this information can be used to develop and test models of binaural hearing.

Experiment 1

The first experiment was a psychoacoustical study on 2 rabbits that were tested over many months. BMLDs were established at two different noise masker levels, and differences in performance across reproducible noise maskers were studied.

All rabbit experimental methods were approved by the Charles River Campus Institutional Animal Care and Use Committee at Boston University.

These methods build on a previous experiment (Carney, Mason, Harrison, Richards, & Idrobo, 1998) and other preliminary work with different animals and experimental paradigms. The previous paradigms, based on the method of constant stimuli, were not adequate in practice to show significant differences in performance across reproducible noises in all cases. The current experimental methods were refined, especially in the matter of stimulus-level selection, to produce reliable and robust results over very long terms of testing individual rabbits. Extensive testing of individual rabbits was required to analyze performance across reproducible noises, which requires a large number of trials, both with and without tones, for each noise waveform.

Method

Subjects. Two 2.0–3.5-kg female Dutch Belted rabbits (R4 and R6) were the subjects for these behavioral experiments. These rabbits were housed in a laboratory animal facility with an ad-lib food schedule and a 12-hour light–dark cycle. R4 was tested for 10 months, and R6 was tested for 15 months. A bar was mounted on the top of the skull with screws and dental acrylic to allow stable head positioning during behavioral sessions. The ear canals were inspected for evidence of ear mites or inflammation. The distortion product otoacoustic emission audiograms (DPOAE audiograms) of both rabbits were obtained with an ILO88 (Otodynamics, Herts, England). These DPOAE audiograms were compared with published rabbit DPOAE audiograms (Lonsbury-Martin, Martin, Probst, & Coats, 1987) as well as with DPOAE audiograms from other rabbits tested in this laboratory, and they were within normal limits.

Sound generation. Acoustic stimuli were generated, attenuated, and mixed with a programmable acoustic system (Tucker Davis Technologies, Gainesville, FL) and were presented through earphones (Beyerdynamic DT 48; Beyerdynamic, Heilbronn, Germany) coupled to soft plastic earmolds custom made for each rabbit. A probe tube microphone (Etymotic ER-7; Etymotic Research, Elk Grove Village, IL) was used to calibrate the acoustic stimuli delivered to the ear canal. Bursts of 64 independent, broadband (20-kHz bandwidth) Gaussian noises were used for acoustic calibration at the beginning of each session. These noises did not include the 10 reproducible noises used in the experiment. The calibration consisted of a measurement of the frequency response of the acoustic system, which included the stimulus system, earphone, earmold, and ear canal.

After at least eight calibration curves were collected for a given rabbit, an average of the calibrations was created. Once this average calibration was created, all subsequent daily calibrations were compared with the average calibration as well as with previous daily calibrations, and any significant discrepancies were investigated and eliminated before testing began. In our experience, calibrations are quite consistent from day to day, with slight variations that may be due to the precise position of the probe tube in the ear canal. The range of measurements of the frequency response at 500 Hz, for example, had a range of ±2–3 dB over the sessions used for the average calibration.

The information at 500 Hz on the average calibration curve was used to set the level of the 500-Hz tones used in the detection task. The average calibration was also used to shape the noise spectra to compensate for the properties of the acoustic system, thus producing noise waveforms with flat magnitude spectra at the ear canal and ensuring that an identical set of waveforms was presented every day. Small differences in the daily calibration due to slight changes in earmold or probe tube position thus did not introduce variance into the stimulus ensemble.

Tones and 10 reproducible Gaussian noises were used during experimental sessions. The tones and the reproducible noises were 500 ms in duration, including the 10-ms $\cos^2$ onset–offset ramps. Noises were generated digitally and were band limited from 100 Hz to 3 kHz. The sound level of the noise masker was set to either a 40-dB spectrum level or a 20-dB spectrum level (equivalent to root-mean-square [rms] levels of 75 and 55 dB SPL, respectively).

During the experimental sessions, noise bursts were delivered every 1.5 s. Tones were presented simultaneously with a noise burst every 49.5 to 70.5 s, or once per minute on average. The intertrial interval varied randomly within this time range from trial to trial.

Training. The unconditioned stimulus (US) was an electrical shock delivered to electrodes (which were either two Med Associates [St. Albans, VT] TD-23 silver–silver chloride electrodes or two wound clips) positioned posterior to the left orbit. The electrical shock was 60 Hz, 0.9 mA, and 100 ms in duration and was delivered 400 ms after the onset of the conditioned stimulus (CS), which was a 500-ms-duration tone. An unconditioned response (UR) was an eyeblink that began after the onset of the shock and therefore was considered to have been elicited by the shock, not the tone. The CS was always paired with the US. A preliminary study investigated other CS–US pairing schedules, and it was found that this method resulted in the most consistent and best performance on the tone-detection task.

The position of the eyelid was monitored by a photodiode–phototransistor pair that was aimed at the edge of a small piece of white paper taped to the rabbit's eyelid. The eyelid-position signal was low-pass filtered with a cutoff frequency of 60 Hz and sampled at a frequency of 1 kHz. The discrete signal was smoothed with a 5-point average and was stored for later analysis. The derivative of the eyelid position signal was compared with a threshold criterion to determine the onset of an eyeblink. An eyelid response was designated a conditioned response (CR) if it began during the tone presentation and before the onset of the shock. Eyeblinks that occurred during the noise-alone presentations were also recorded and analyzed.

A tracking procedure was used during rabbit testing (Martin, Lonsbury-Martin, & Kimm, 1980; Rosenberger, 1970). The 50% correct level was targeted in a one-up, one-down paradigm (Levitt, 1971) to study performance at the lowest possible tone level without extinguishing the CR. Studying responses at the 50% correct level also avoided the floor and ceiling effects that eliminate the effect of using different reproducible noise maskers. In this paradigm, the level of the CS was reduced one step size (2 dB) after a tone trial with a CR and increased one step size after a tone trial with no CR. The trials that resulted in reversals (a change of track direction) were extracted, and the mean of the tone levels at an even number of reversals was computed to determine the tone level for 50% correct detection. We omitted the first four or five reversals (depending on whether there was an odd or even number of reversals overall) of the track when calculating the mean of the reversal levels of the track. Different step sizes were tested in a preliminary study, and it was found that the 2-dB step size resulted in consistent measurements of performance with a practical step size. Once underway, the lowest tone level of the track was determined by the rabbit's performance, and the loudest tone level was limited to 86 dB SPL.

The tracking method of determining sensitivity was selected on the basis of the results of a previous study (Carney et al., 1998) as well as on a preliminary study in other rabbits that compared this method with other methods of choosing CS level. For example, using the method of constant stimuli (Carney et al., 1998), in which tone levels were fixed for a block of 10 trials and then changed by the experimenter for the following block on the basis of the rabbit's performance, it was difficult to maintain the animal at a 50% performance level with a fixed stimulus level. Instead, a one-up, one-down tracking procedure was adopted. This tracking procedure was highly successful in maintaining consistent performance throughout 2-hour daily sessions and over several months of testing.

Testing procedure. In preliminary testing, Pavlovian conditioning was used to train the rabbit to respond to tones in quiet. Tones were delivered at 70 dB SPL and assumed to be suprathreshold, on the basis of published rabbit audiograms (Heffner & Masterton, 1980; Martin et al., 1980) and on the basis of preliminary studies performed in this laboratory. Training continued until the percentage of CRs was at least 80% over a 2-hr session of approximately 80 trials. After each block of 10 tone trials, the rabbit was given a 1–3-min break. The next step was to introduce tracking of the CS level to the tones-in-quiet task with the procedure described above. Tracking of tone levels in quiet continued for at least three sessions.

Once the rabbit was trained to respond to tones in quiet, 10 reproducible noises were added as noise maskers. Daily testing sessions consisted of a single 2-hr track of approximately 3,000–3,500 noise-alone presentations and 80–90 noise-plus-tone trials. When a 40-dB noise masker was used, tone levels started at 70 dB SPL; when a 20-dB noise masker was used, tone levels started at 60 dB SPL. The noise for each trial was randomly chosen from the set of 10 reproducible noises. The tone frequency was fixed at 500 Hz, and tone level was controlled by the tracking procedure described above. Conditions with a 40-dB noise level were tested for many consecutive sessions until there were enough trials to establish differences in performance across reproducible noise waveforms.

Data analysis. The psychometric functions for each condition were extracted from the tracks (Dai, 1995), and a curve was fitted to the data with a weighted version of the following logistic function (Hall, 1981):

$$P(x) = \frac{1}{2}\left(1 + \frac{1 - P_L}{1 + e^{-a(x-m)}}\right),$$

where a is the slope of the function and m is the midpoint of the function. The lapse coefficient, P_L, is a measure of the difference between perfect performance and the rabbit's asymptotic performance for a given condition. Given the frequency of the CSs (which averaged once per minute), it is not unusual for an animal's performance to asymptote at less than 100% (Mitchell, 1973).

Because a tracking procedure was used, the number of trials at the lowest and highest ends of the psychometric function comprised a low percentage of the total number of trials. Therefore, only tone levels that were presented more than 20 times were used in the curve fits (such that each trial had an effect of 5% or less on the percentage at that level). Each level around the 50% point of the psychometric function had 350–600 tone trials for the data sets collected at the 40-dB noise level.

The BMLD was estimated on the basis of the difference in performance across the N_0S_0 and N_0S_π stimulus conditions in two different ways. One estimate was made with the difference between the means of the track reversals, which is the difference in tone levels required for 50% correct performance. However, this performance level is well above the spontaneous blink rate for rabbits and therefore may be a conservative estimate of the rabbit's sensitivity to tones. For this reason, the average across sessions of the lowest tone levels that resulted in a CR was used as a measure of the rabbit's sensitivity. The difference in sensitivity across stimulus conditions was then used as a second estimate of the BMLD. These two measures of the BMLD were generally consistent, and both are reported below.

Because spontaneous blinks in the rabbit are seldom (1–3 per hour [Gormezano, 1966]), eyeblinks that occurred during noise-alone trials were monitored closely and analyzed for significant dependence on the reproducible noises with the same chi-square test as was used for tone trials. Eyeblinks occurred on fewer than 3% of noise-alone presentations. These responses were analyzed in the context of the binaural condition in which they were made and are therefore designated as N_0S_0 and N_0S_π responses even though these trials did not include tonal stimuli.

To prevent reporting a response at a low level that was in fact due to spontaneous movements of the rabbit, the local eyeblink response rate was taken into consideration when measuring sensitivity. If an eyeblink response occurred within the 10 noise-alone presentations before or after a tone trial (i.e., the local eyeblink response rate was greater than 5%), then the result of the tone trial was discarded for the sensitivity analysis. In the data presented, discarding of trials was infrequent and the maximum number of discards was two trials in a session. The average across sessions of the lowest tone levels resulting in a CR was then expressed as a signal-to-noise ratio to compare the rabbits' sensitivity with that of other species. The signal-to-noise ratio (E/N_0) was calculated as

$$\frac{E}{N_0} = \text{Average lowest tone level (dB SPL)}$$

$$- \text{Noise spectrum level (dB SPL)} + 10\log_{10}\frac{\text{duration (s)}}{1\ \text{s}}.$$

The duration is the time that the rabbit had to respond for its response to be considered a CR. In this analysis, a duration of 0.4 s was used, which was the entire duration of the CS before the US began. Because the rabbit actually had less than 400 ms in which to begin its eyeblink response, this correction for duration leads to a conservative estimate of E/N_0.

In many psychophysical tasks, sensitivity is described in terms of the metric d', which is computed as the difference in mean performance across stimulus conditions, normalized by the variance. The value of d' may be used to determine whether the signal level is appropriate for a given listener, and the signal level may be adjusted until a d' of unity is reached. In Pavlovian conditioning, the occurrence of tone trials must be kept relatively low to maintain the salience of the tone. In our case, approximately 1 out of 45 noise trials had an added tone and the percentage of CRs had to be held at 50% or higher (to avoid extinguishing). In contrast, the probability of responses on the noise-alone trials was very low (typically less than 3%). This discrepancy in response probabilities between tone-plus-noise and noise-alone trials leads to very high values of d' that are not useful for evaluation of performance.

The trials at tone levels around the 50% point of the psychometric function were used to analyze the differences in performance across reproducible noise masker. Differences in performance across noise waveforms would not be apparent at very high or low tone levels. The trials at tone levels at or just below the 50% point on the psychometric function as well as the trials at tone levels one step (2 dB) up and down from this level were sorted according to the reproducible noise sample. The percentage of CRs was then calculated for each reproducible noise masker. If the reproducible noise masker affected performance on the tone-detection task, then there should have been a range of performance across waveforms; that is, some noises should have resulted in a low percentage of CRs and others should have resulted in a high percentage.

Differences in performance from noise to noise were analyzed for significance with a chi-square test (Siegel & Colburn, 1989). This test determines whether the variation in performance across noises is greater than would be expected on the basis of Bernoulli sampling variability. An alpha level of .01 was used for all chi-square tests. Statistical power (Cohen, 1969, 1992) was also calculated. This measure takes into account the n of each noise sample, not just the average n, as in the chi-square test.

Results

BMLDs. BMLDs were demonstrated in both rabbits at two different noise masker levels, 20-dB and 40-dB spectrum levels. Figure 1 shows a partial data set (for clarity in seeing the individual tracks) used to determine the BMLD for a rabbit (R4) when a 40-dB noise masker was used. The upper tracks with the filled squares are two N_0S_0 sessions for this rabbit, and the lower tracks with the asterisks are two N_0S_π sessions. It is clear that the binaural cues in the N_0S_π condition allowed the rabbit to track to lower tone levels than in the N_0S_0 condition. Thus, the rabbit's BMLD is illustrated in this figure by the vertical separation between the two sets of tracks.

Psychometric functions were extracted from the rabbit tracking data and fitted with a weighted logistic function as described above. Figure 2 shows the psychometric functions for both rabbits and noise levels. The lapse, or difference between perfect performance and asymptotic performance, varied between rabbits and conditions in a nonsystematic way. The BMLD in the psychometric functions is the horizontal shift between the proportion of CRs for N_0S_0 and N_0S_π at the 50% point.

BMLDs of 7.4 dB (R4) and 7.0 dB (R6) were measured at the 20-dB noise masker level, and BMLDs of 9.5 dB (R4) and 8.4 dB (R6) were measured at the 40-dB noise masker level when calculated as the difference between the means of the track reversals (see Figure 1). E/N_0 was used as a sensitivity measure and calculated from the average of the lowest tone levels resulting in CRs. The average E/N_0 for the 2 rabbits with the N_0S_0 condition was 18.2 ± 0.2 dB when a 20-dB noise masker was used and 18.8 ± 0.8 dB when a 40-dB masker was used. Average E/N_0 was 11.6 ± 0.9 and 10.4 ± 1.6 for the N_0S_π condition with 20-dB and 40-dB noise maskers, respectively (see Table 1, rows 1 and 2).

Results of reproducible noise analysis. The chi-square test confirmed significant differences in performance across noise waveforms for the rabbits with the 40-dB reproducible noise maskers (see Table 2).

Figure 3 shows the percentage of responses to tone-plus-noise and noise-alone presentations across noise maskers for the 2 rabbits and stimulus conditions, N_0S_0 and N_0S_π. The performance across noises in this figure shows that the influence of the reproducible noise on performance was greater for R4 than for R6. For example, in the N_0S_0 condition, R4's performance ranged from 15% to 64% correct depending on the reproducible noise masker, whereas R6's performance ranged from 39% to 60% correct.

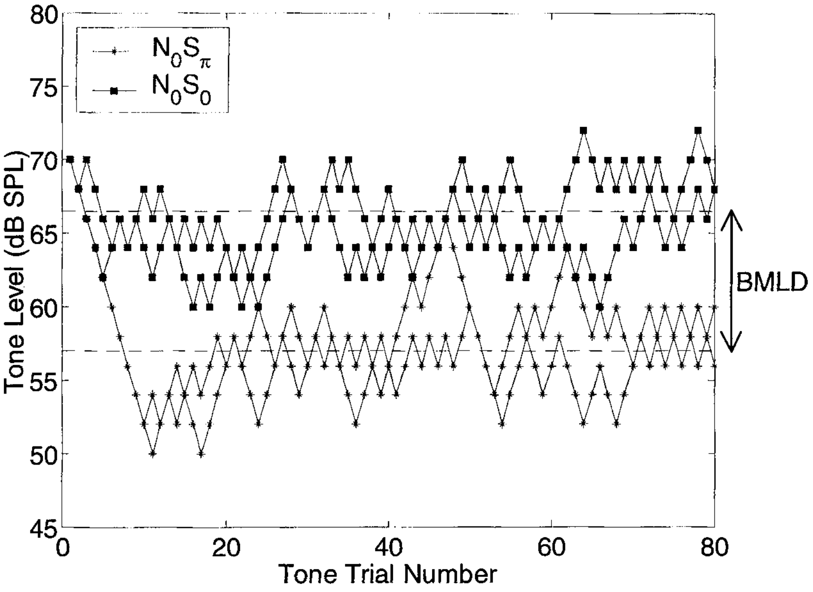

Figure 1. Four tracks representative of the set of tracks used to determine R4's binaural masking level difference (BMLD) for a 40-dB noise masker. The BMLD was calculated as the difference between the means of the reversals (represented by the dashed lines).

The performance across waveforms for the 20-dB noise level data (not shown) was less influenced by the reproducible noise maskers, although some conditions did result in significant differences across reproducible noise waveforms (see Table 2). Fewer sessions were run at the 20-dB noise level (N_{R4} = 13 sessions, N_{R6} = 16 sessions) than were run at the 40-dB noise level (N_{R4} = 44 sessions, N_{R6} = 56 sessions) because the goal of the 20-dB sessions was to establish the BMLD at that level. The limited number of trials per noise for the 20-dB noise level data reduced the value of the chi-square statistic. Analyses of performance across reproducible noises were focused on the 40-dB noise level, for which many more trials were collected.

Correlation coefficients were examined for the data sets collected at a 40-dB noise masker level, and an alpha level of .05 was used for the correlation tests. Three comparisons were made: (a) correlation of performance across reproducible noises for the N_0S_0 condition and the N_0S_π condition (see Table 3, columns 2 and 3), (b) correlation of the performance across reproducible noises for the responses to tone-plus-noise trials and the responses to noise-alone presentations (see Table 3, columns 4 and 5), and (c) the intersubject correlation of performance across reproducible noises (see Table 4).

In addition to calculating correlation coefficients, a visual comparison across conditions and subjects is useful for evaluating the similarity of the performance across reproducible noises (see Figures 3 and 4). For example, Figure 3 shows that when Noise Sample 8 was used as a masker, there was a relatively high probability of a CR for both conditions and both rabbits.

Correlation of N_0S_0 and N_0S_π performance. A significant correlation was found between N_0S_0 and N_0S_π performance across reproducible noises for the rabbits' responses to tone-plus-noise trials (Table 3, column 2). Because R6's responses were less influenced by the noise maskers, a lower correlation coefficient between the two conditions is not surprising. Both rabbits had significantly correlated responses to noise-alone presentations across the two conditions (Table 3, column 3).

Correlation of tone-plus-noise and noise-alone performance. The correlation across reproducible noise waveforms between the rabbits' responses to tone-plus-noise trials and their responses to noise-alone presentations was not significant when performing the N_0S_0 task (see Table 3, column 4) and was significant for 1 rabbit performing the N_0S_π task (see Table 3, column 5).

Intersubject correlation. When the performance across reproducible noises of the 2 rabbits was compared with each other, their responses to the tone trials were significantly correlated for the N_0S_0 condition (see Table 4, column 2) but not for the N_0S_π condition (see Table 4, column 3). The responses across reproducible noises to noise-alone presentations were significantly correlated between R4 and R6 for the N_0S_π condition but not for the N_0S_0 condition (see Table 4).

Discussion

BMLDs and significant differential responses across reproducible noise samples were shown in 2 rabbits with the stimuli described above. These results demonstrate that a Pavlovian conditioning paradigm can be adapted for use in psychophysical studies. However, the variations in performance across reproducible noises in the rabbits was somewhat reduced as compared with previous reports in human listeners (discussed below). To ascertain that the difference between human and rabbit performance was not due to our choice of stimulus parameters, we conducted a limited study (Experiment 2) with human listeners using the same stimuli as in Experiment 1.

The reduced variation in performance across reproducible noises in the rabbit might have been due to the use of relatively long (500 ms) noises. Large differences in the features of short-duration, randomly

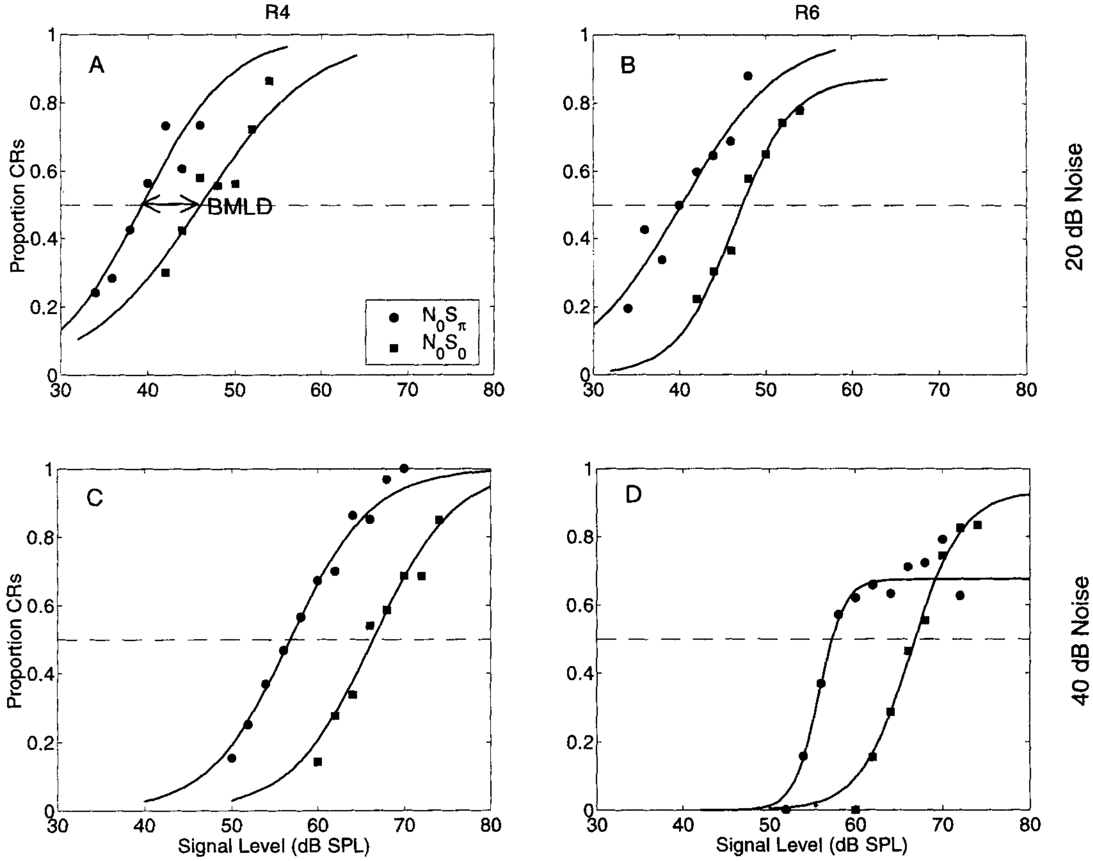

Figure 2. Psychometric functions for 2 rabbits at two noise masker levels. Each graph shows two logistic psychometric functions, corresponding to the N_0S_0 condition and the N_0S_π condition, that were fitted to the data (solid line). The dashed line is at the 50% level of the psychometric functions and is shown for reference. A: Rabbit R4, 20-dB noise masker. Tone levels at 50% performance level: N_0S_0 = 46 dB SPL; N_0S_π = 39 dB SPL. B: Rabbit R6, 20-dB noise masker. Tone levels at 50% performance level: N_0S_0 = 47 dB SPL; N_0S_π = 40 dB SPL. C: Rabbit R4, 40-dB noise masker. Tone levels at 50% performance level: N_0S_0 = 66 dB SPL; N_0S_π = 57 dB SPL. D: Rabbit R6, 40-dB noise masker. Tone levels at 50% performance level: N_0S_0 = 67 dB SPL; N_0S_π = 57 dB SPL. BMLD = binaural masking level difference; CR = conditioned response.

selected Gaussian noise waveforms may occur. However, one might expect increased duration to reduce the variation in tone detection across reproducible noises; therefore, humans were tested with these stimuli in Experiment 2. Previous studies with reproducible noises in human listeners used shorter duration noises (e.g., 100 ms [Gilkey et al., 1985]; 340 ms [Bernstein et al., 1998]). In the rabbit study, 500-ms duration noises, with a CS–US interval of 400 ms, were chosen on the basis of studies of Pavlovian conditioning of the rabbit eyeblink (Frey & Ross, 1968).

Experiment 2

Psychoacoustical experiments were performed with 3 human listeners using the same reproducible stimulus waveforms as were used for Experiment 1 to ensure that results comparable to previous human studies could be obtained with these stimuli. This experiment was limited to a study of the variability in responses across reproducible noises; the BMLD has been reported in a number of previous studies of human listeners (reviewed by Durlach & Colburn, 1978).

Method

Experiments with human listeners were approved by the Boston University Charles River Institutional Review Board.

Subjects. Three unpaid volunteers without hearing impairment and between the ages of 19 and 24 completed the tone-in-noise detection study.

Sound generation. Tones and the same set of 10 reproducible noise maskers used in Experiment 1 were generated, attenuated, and mixed with the same model of Tucker Davis Technologies programmable equipment as in Experiment 1. Listeners were tested in an Industrial Acoustics (Bronx, NY) double-walled, sound-attenuating booth, as in Experiment 1.

Testing procedure. Preliminary training sessions with a two-alternative, two-interval forced-choice tracking procedure were used to adjust the tone to a level appropriate for a subsequent fixed-level, one-interval yes–no task. In the one-interval task, the listener responded by keyboard after each trial that either "yes, the tone was present" or "no, the tone was not present." The practice sessions used random wideband noise, ensuring that the listeners had no experience with the reproducible noises before the yes–no runs. Both the preliminary sessions and the yes–no task gave feedback to the listener after every trial.

Each run of the yes–no task consisted of 100 trials that contained either the reproducible noise alone or the reproducible noise and a 500-Hz tone

Table 1
BMLD and E/N_0 Values for Five Species

Species	Noise level (dB)	BMLD	E/N_0	
			N_0S_0	N_0S_π
Rabbit (present study)				
Spectrum Level 1	40	9[a]	19	10
Spectrum Level 2	20	7[a]	18	12
Human (Bernstein et al., 1998)[b]	50	14	10	−4
Cat (Wakeford & Robinson, 1974)[c]	44	8[d]	13[d]	5[d]
Ferret (Hine et al., 1994)[e]	44, 50[f,g]	10	11	1
Budgerigar (Dent et al., 1997)[e]	22, 28[f,h]	5	15[i]	10[i]

Note. Unless otherwise specified, these experiments used 500-Hz tones and wideband noise maskers. BMLD = binaural masking level difference; E/N_0 = signal-to-noise ratio.
[a] The BMLDs reported for the present study were measured as the difference between the mean levels of performance for the N_0S_0 and N_0S_π conditions; similar estimates of the BMLD would result from the difference in E/N_0 values (see Figure 1A). [b] The noise maskers were gated such that they were 40 ms longer than the tones. [c] This study used continuous noise and 1.5-s tones. [d] These values are from Fay's (1988) extractions. [e] These studies used free-field stimuli. The one-speaker (unilateral) condition is reported here as N_0S_0, and the two-speaker (bilateral) condition as N_0S_π. [f] Continuous noise was used in these studies. The first spectrum level is for the one-speaker condition, and the second spectrum level is for the two-speaker condition. [g] Narrowband (120-Hz bandwidth) noises were used. [h] 1-kHz tones were used. [i] This study reported signal-to-noise ratios at masked threshold, which are the values in the E/N_0 columns.

at the predetermined level. Stimuli were presented to the listener through TDH-39 headphones (Telephonics, Farmingdale, NY). Participant 1 (P1) was tested at tone levels of 54 and 42 dB SPL, Participant 2 (P2) at 55 and 43 dB SPL, and Participant 3 (P3) at 57 and 39 dB SPL for the N_0S_0 and N_0S_π conditions, respectively. Noise-alone and noise-plus-tone presentations were equally probable; therefore, chance performance was 50% correct. The 10 reproducible noises had a 2900-Hz bandwidth (100 Hz to 3 kHz), 500-ms duration, and 40-dB spectrum level. As is standard in human psychoacoustical experiments with headphones, the acoustic stimuli were not corrected for each individual. (It was the use of earmolds sealed into the ear canal that necessitated spectral correction in the rabbit experiment.) During a run, the 10 reproducible noises were presented in random order and each noise was presented 10 times—5 times with a tone and 5 times alone. Ten runs were performed for each stimulus condition for each listener.

Data analysis. As in Experiment 1, differences in performance from noise to noise were analyzed for significance with a chi-square test, and an alpha level of .01 was used for all chi-square tests.

Results

Results of reproducible noise analysis. Figure 4 shows the percentage of responses to tone-plus-noise and noise-alone presentations across noise maskers for the 3 listeners and two stimulus configurations, N_0S_0 and N_0S_π. The variation of responses across

Table 2
Results of Reproducible Noise Analysis for 2 Rabbits and Two Noise Masker Levels

Condition and rabbit	40-dB noise			20-dB noise		
	Total no. of trials	χ^2	Power	Total no. of trials	χ^2	Power
Tone-plus-noise trials						
N_0S_0						
R4	865	85.9**	.99	245	15.1	.39
R6	1,554	28.2**	.68	352	16.0	.51
N_0S_π						
R4	1,007	62.3**	.95	301	27.2**	.75
R6	1,398	29.3**	.77	423	9.7	.33
Noise-alone trials						
N_0S_0						
R4	61,673	187.5**	.99	18,510	32.2**	.98
R6	106,075	85.7**	.99	24,204	7.8	.46
N_0S_π						
R4	68,508	211.8**	.99	21,152	63.0**	.99
R6	85,181	69.8**	.99	31,071	16.9	.80

Note. Power was calculated as specified by Cohen (1969, 1992).
** $p < .01$.

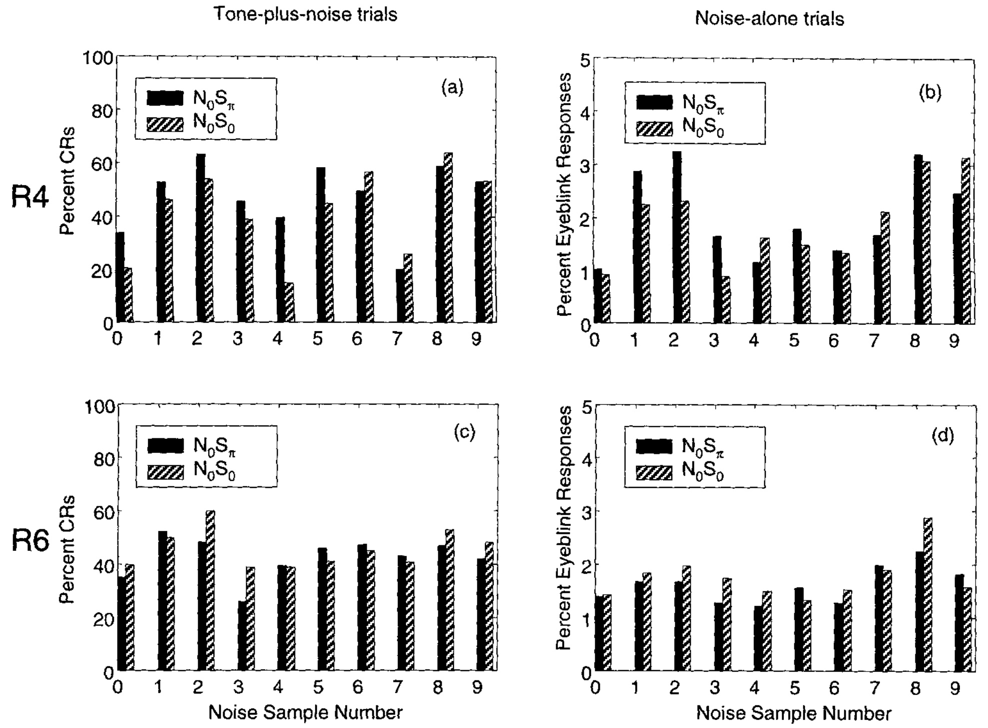

Figure 3. Percentage correct on tone-plus-noise presentations (a, c) and percentage of eyeblink responses on noise-alone presentations (b, d) for 2 rabbits (R4, R6). Filled bars show the N_0S_π results, and hatched bars show the N_0S_0 results. The noise level was 40 dB. Note that the responses to noise-alone presentations are segregated according to the binaural condition in which they were collected. CR = conditioned response.

noises demonstrates the strong effect that the different noise maskers had on the listeners' performance. The chi-square test confirmed significant differences in performance across noise waveforms (see Table 5). As in Experiment 1, correlation coefficients were examined, and an alpha level of .05 was used for the correlation tests.

Correlation between N_0S_0 and N_0S_π performance. P1's and P3's tone-plus-noise data were not correlated between the N_0S_0 and N_0S_π conditions, whereas P2's data were correlated (see Table 3, column 2). As is apparent from the similarities in performance across noise waveforms in Figure 4, listeners' responses to noise-alone presentations across noise waveforms were significantly correlated between the N_0S_0 condition and the N_0S_π condition (see Table 3, column 3).

Correlation between tone-plus-noise and noise-alone performance. This comparison in human listeners revealed a significant correlation for 2 of the 3 listeners for the N_0S_0 condition (see

Table 3

Correlations Across Reproducible Noise Maskers

	r between N_0S_0 and N_0S_π		r between tone-plus-noise and noise-alone trials	
Subjects	Tone plus noise	Noise alone	N_0S_0	N_0S_π
Rabbits				
R4	.79*	.78*	.54	.67*
R6	.64*	.76*	.57	.46
Humans				
P1	.18	.63*	.91*	.40
P2	.83*	.93*	.63*	.79*
P3	.61	.88*	.53	.38

Note. All correlation coefficients had eight degrees of freedom.
$^* p < .05$.

Table 4

Intersubject Comparisons of Performance Across Reproducible Noises

Stimulus condition and subject	r: N_0S_0	r: N_0S_π
Intersubject correlations: Rabbits		
Tone plus noise: R4–R6	.72*	.43
Noise alone: R4–R6	.61	.70*
Intersubject correlations: Humans		
Tone plus noise		
P1–P2	.92*	.10
P1–P3	.76*	.74*
P2–P3	.75*	.07
Noise alone		
P1–P2	.72*	.74*
P1–P3	.75*	.88*
P2–P3	.69*	.56

$^* p < .05$.

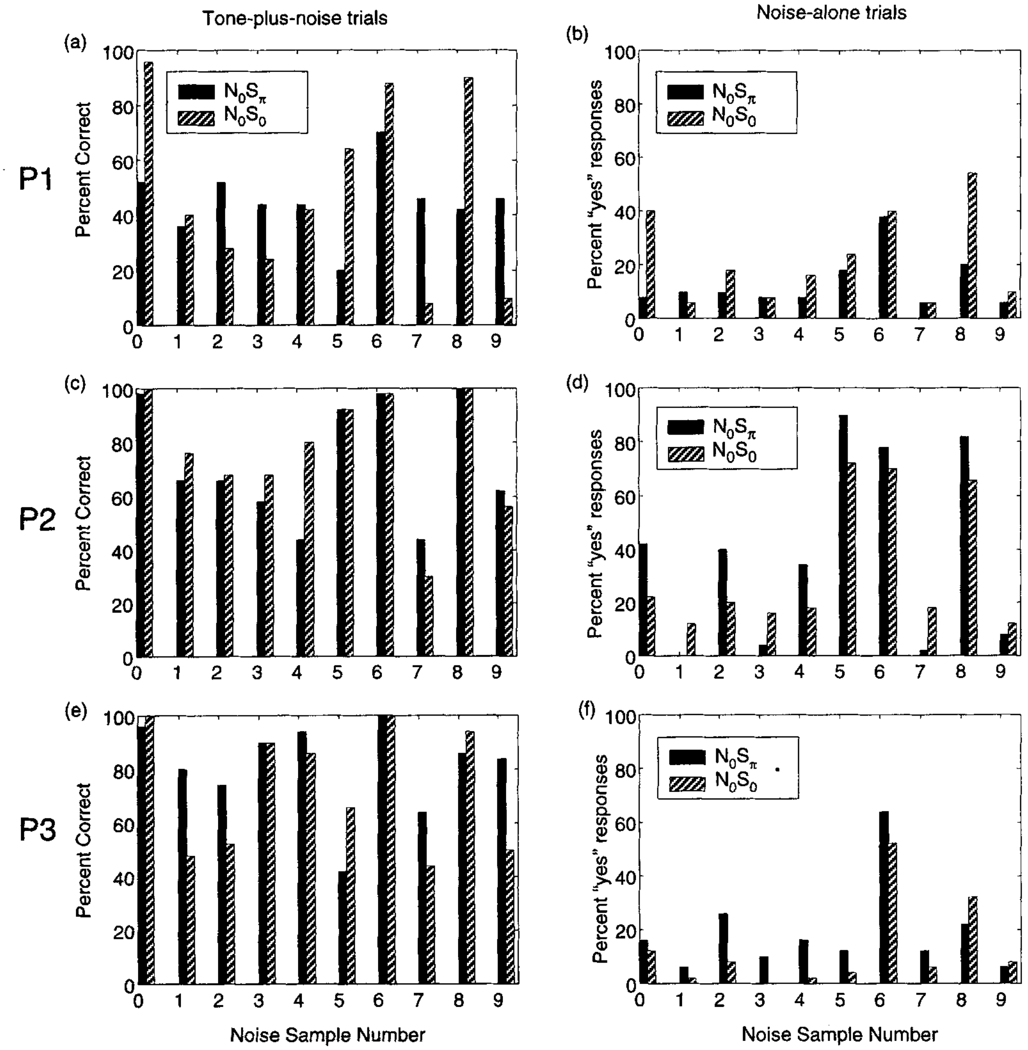

Figure 4. Percentage correct on tone-plus-noise presentations (a, c, e) and percentage of "yes" responses on noise-alone presentations (b, d, f) for 3 human listeners (P1, P2, P3) for the same 10 reproducible noise waveforms used in Experiment 1. Note that the responses to noise-alone presentations are segregated according to the binaural condition in which they were collected.

Table 3, column 4) and for only 1 of the 3 listeners for the N_0S_π condition (see Table 3, column 5).

Intersubject correlation. As Figure 4 suggests, most of the human listeners' differential responses across reproducible noise masker were significantly correlated across listeners. The responses to tone-plus-noise trials and responses to noise-alone presentations were correlated for the N_0S_0 condition across all listeners (see Table 4, column 2). However, the correlation between listeners was not as strong for the N_0S_π condition, particularly when comparisons were made with P2 (see Table 4, column 3).

Discussion

The goal of Experiment 2 was to ensure that the stimuli used in Experiment 1 would result in the same variations across reproducible noises as seen in previous human studies. The longer stimulus

Table 5
Results of Reproducible Noise Analysis for 3 Human Listeners

	χ^2	
Condition and participant (P)	Tone plus noise	Noise alone
N_0S_0		
P1	96.7***	73.2***
P2	125.0***	131.2***
P3	121.9***	21.1*
N_0S_π		
P1	28.5***	38.0***
P2	110.5***	230.3***
P3	86.9***	83.4***

Note. Each chi-square result is based on 50 trials per reproducible noise of the given condition (N_0S_0 or N_0S_π, tone plus noise or noise alone).
$^* p < .05$. $^{***} p < .001$.

duration might be expected to reduce the amount of variation across noises. However, the variation in performance across reproducible noises for human listeners was comparable to that reported in previous studies, despite the use of 500-ms tones and noises.

General Discussion

In Experiment 1, a Pavlovian conditioning paradigm was used to establish two psychoacoustical phenomena in the rabbit: the BMLD and differential performance on a tone-detection task across reproducible noise maskers. In addition, Experiment 2 was conducted in the same laboratory with the same reproducible noises to confirm that the stimuli used in Experiment 1 resulted in differences across reproducible noises in humans comparable to those in previous studies.

The size of the BMLDs in the rabbit was comparable to that of other animals, including humans (see Table 1). The smaller BMLD with a 20-dB noise masker, as compared with that of a 40-dB noise masker, is a trend also seen in human data (Durlach & Colburn, 1978). The signal-to-noise ratio, expressed as E/N_0, was elevated compared with other species (see Table 1). This elevation in signal-to-noise ratio may have been due to differences in the auditory system between the rabbit and the other species studied with this task or due to the use of the Pavlovian conditioning paradigm. Also not considered here is the effect of masker presentation. The use of continuous noise, as in the ferret, cat, and budgerigar studies, has been shown to slightly improve masked thresholds (Wier, Green, Hafter, & Burkhardt, 1977). An even greater difference in masked threshold is seen when the gated masker is longer than the signal, creating a masker "fringe" (Carlyon, 1987) as was used in the Bernstein et al. (1998) study. The use of simultaneously gated noises and tones in the current study may have reduced the E/N_0 relative to other studies. However, E/N_0 is generally elevated in other species when compared with humans (Fay, 1988), and further studies in the rabbit should help to clarify this issue. The consistent performance over a long time period and the similarity in the trends of the results between the rabbit and other species (see Table 1) suggests that this paradigm will prove useful for simultaneous physiological experiments examining the individual differences seen with the reproducible noise stimuli.

The 2 rabbits in this study performed Pavlovian conditioning experiments for several months in a stimulus paradigm that included tone-level tracking, which effectively changes the CS from trial to trial. This continual change in the CS may have contributed to the elevated E/N_0 values measured with this paradigm; however, it did not compromise the rabbits' ability to perform in a Pavlovian conditioning experiment. To our knowledge, this is the first use of Pavlovian conditioning over such an extended time period to study psychoacoustical phenomena. The robustness of the paradigm was especially critical for the study of differences in performance across different samples of noise, which required analysis of results over many sessions.

Clear differences were seen across reproducible waveforms for both the human listeners and the rabbits, but these differences were not necessarily correlated across subjects (see Table 4). This finding was also reported in previous studies (Gilkey et al., 1985; Isabelle & Colburn, 1991) and has been attributed to the presence of redundant cues within the stimulus. The redundancy allows the use of different strategies when performing the task, and strategies may differ between listeners (Isabelle, 1995).

The individual comparisons of noise-alone presentations between the N_0S_0 and N_0S_π conditions were significantly correlated for all subjects, both rabbit and human. This result was expected because the 10 noise waveforms (without the CS) were identical across conditions. Not all subjects had correlated performance across conditions for their responses to tone-plus-noise trials, perhaps because the stimuli differed for these two conditions due to the phase shift of the S_π tone. A more complete study that includes N_0S_0 stimuli with tones added in 0° phase and 180° phase is required to further investigate relationships between N_0S_0 and N_0S_π responses (Gilkey et al., 1985).

The significant correlation across reproducible noises of the responses to noise-alone presentations across the N_0S_0 and N_0S_π conditions for both the rabbits and the humans and the weaker correlation of responses to tone-plus-noise presentations across these conditions (see Table 3, column 2) was a trend seen in a previous study of humans performing a tone-detection task in the presence of reproducible noise maskers (Gilkey et al., 1985). However, the values of the correlation coefficients were higher overall in the previous study, which may be related to the higher noise level used in that study (50-dB SPL spectrum level).

The correlation between the performance on reproducible noises for the responses to tone-plus-noise trials and that for noise-alone presentations was not significant in most of the rabbits and human listeners tested. However, the interactions between the tone and the individual noise masker that influence the probability of a response are not well understood. This difference in performance across individuals motivates the development of a paradigm that will allow the study of both behavioral and physiological responses in individual rabbits.

The ability to study the behavior and physiology of psychoacoustical phenomena in the same subject may lead to further insight into binaural processing and its modeling. Previous physiologically motivated models, which focused on cross-correlation, were able to explain the general phenomenon of the BMLD (Colburn, 1977) but were not successful at predicting differences in performance on individual reproducible noise maskers (Isabelle, 1995). Physiological experiments using the same stimuli and animals as behavioral experiments should allow determination of specific noise properties that are correlated to neural and behavioral responses, and the rabbit has proven to be a suitable animal for physiological experiments in an awake preparation (e.g., Kuwada, Stanford, & Batra, 1987). This information will provide new hypotheses for the development and testing of binaural models. In ongoing work, an updated model of the auditory periphery (Zhang, Heinz, Bruce, & Carney, 2001) is being used to provide input to binaural models in a study of the BMLD and reproducible noise results (Evilsizer, 2000).

Additional explanation of the BMLD and the effects of reproducible noise maskers may be relevant for explaining the difficulty experienced by hard-of-hearing listeners in understanding speech in a noisy setting. For example, it was recently shown (Hawley, 2000; Hawley, Litovsky, & Colburn, 1999) that performance on a BMLD task with a wideband noise as a masker is a good predictor of performance on a speech-based task in a complex environment for both hard-of-hearing listeners and those with normal hearing.

This finding provides further motivation for understanding the physiological basis of the BMLD.

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