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Detection and discrimination of natural calls in masking noise by birds: estimating the active space of a signal

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We tested the ability of birds to detect and discriminate natural vocal signals in the presence of masking noise using operant conditioning. Masked thresholds were measured for budgerigars, *Melopsittacus undulatus*, and zebra finches, *Taeniopygia guttata*, on natural contact calls of budgerigars, zebra finches and canaries, *Serinus canaria*. Thresholds increased with increasing call bandwidth, the presence of amplitude modulation and high rates of frequency modulation in calls. As expected, detection thresholds increased monotonically with background noise level. Call detection thresholds varied with the spectral shape of noise. Vocal signals were masked predominantly by noise energy in the spectral region of the signals and not by energy at spectral regions remote from the signals. In all cases, thresholds for discrimination between calls of the same species were higher than thresholds for detection of those calls. Our data provide the first opportunity to estimate distances over which specific communication signals may be effective (i.e. their 'active space') using masked thresholds for the signals themselves. Our results suggest that measures of peak sound pressure level, combined with the spectrum level of noise within the frequency channel having the greatest signal power relative to background noise, give the most similar results for estimating a signal's maximum communication distance across a variety of sounds. We provide a simple model for estimating likely detection and discrimination distances for the signals tested here.

The ability to communicate is limited by the distance over which a signal can be perceived by a receiver over a background of noise in a particular habitat. This distance has been termed the 'active space' of a signal (Marten & Marler 1977; Brenowitz 1982; Klump 1996). Considerable acoustic noise arises from biotic, abiotic, and increasingly, anthropogenic sources. The ubiquitous nature of this noise has led to much speculation as to whether such noise limits the active space of calls and songs produced by birds (Klump 1996). It also has been suggested that species-specific acoustic signals may be designed to maximize their audibility to conspecifics in certain environments (Marten & Marler 1977; Brenowitz 1982; Wiley & Richards 1982). To date, there has been little direct empirical evidence on any of these points because such studies are difficult to conduct in the field. By contrast, a large number of laboratory studies have examined detection abilities for sounds in noise in a variety of vertebrates, but for the most part these studies have used simple stimuli such as pure tones and broadband 'white' noise (for review see Fay 1988; Dooling et al. 2000).

Laboratory studies with simple stimuli such as pure tones do provide a first approach to estimating the active space of a signal. The concept of a critical ratio comes from determining thresholds of tones in noise, and is the ratio of the power in a pure tone to the power in a noise when a tone is just masked (i.e. becomes inaudible) by the noise (Scharf 1970). For all species in which it has been measured, the critical ratio varies with frequency but remains constant over a fairly wide range of noise levels. That is, a 10-dB increase in the level of noise results in a 10-dB increase in the signal detection threshold. Critical ratio functions have now been measured for a number of mammals and 14 species of birds (Dooling et al. 2000; Wright et al., in press). As is typical of mammals, critical ratios in most birds increase monotonically with frequency by about 3 dB per octave, although there are some exceptions (Fay 1988; Dooling et al. 2000; Wright et al., in press). Comparing the critical masking ratio functions across a bird's hearing range with the frequency spectrum of vocal signals provides a crude estimate of the distance over which those signals might be detected for a given background noise level. The validity of this estimate depends on many factors including the intensity with

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which the sender vocalizes, the location of the sender, and the sound-attenuating properties of the environment, among others. This estimate also assumes that thresholds in noise for complex sounds such as vocalizations are like those of pure tones. However, while energy in a pure tone is concentrated within a single channel of a bird's auditory system, energy in calls and songs may be spread over many channels, or bands, of the bird auditory system (Klump 1996; Dooling et al. 2000). Unfortunately, very little is known from laboratory studies about the effects of noise on the detection of complex sounds by birds, particularly for natural communication signals (Klump 1996).

Another issue concerns the characteristics of noise in natural habitats, which is typically quite different in its spectral shape and temporal patterning from the flat broadband ('white') noise usually employed in laboratory masking experiments (Wiley & Richards 1982; Klump 1996). Two general principles of auditory masking in vertebrates are that energy in the spectral region of the signal contributes more to masking than energy remote from the signal, and the effects of masking are asymmetrical, spreading more from low to high frequencies than the reverse (Egan & Hake 1950; Moore 1997). Natural environmental noise characteristically contains more energy at lower frequencies than flat noise, and a proper estimate of a bird's active acoustic space must incorporate information about thresholds for vocal signals in noise that simulates such a spectral shape. Here we specifically test the masking effectiveness of noises of two different spectral shapes: 'flat' noise with equal energy across the frequency spectrum, and 'traffic' noise with greater energy at lower compared to higher frequencies. Traffic-spectrum noise served as our alternative model for three reasons. First, traffic noise has been well studied for many years, and there is a well-developed literature on the spectral properties and shapes of this type of noise (Warring 1972; Cunniff 1977; Bowlby 1991). Second, traffic noise is similar in shape to wind-generated noise in deciduous temperate oak forests and grasslands (Brenowitz 1982; Ryan & Brenowitz 1985; Klump 1996), allowing us to make comparisons with likely call detection abilities in some natural habitats. Finally, traffic noise is weighted towards lower frequencies (<1400 Hz). In mammals, noise energy concentrated in lower frequencies can have masking effects on higher-frequency channels due to the upward spread of masking (Moore 1997), while the reverse is less likely to be true. By using noise shaped like that generated by vehicles on highways, we hope to provide data that will more accurately simulate the noise found in natural habitats, and that may have practical benefit for estimating the effect of one type of anthropogenic noise on avian acoustic communication.

In estimating communication distances for avian signals in natural habitats, one must consider a bird's ability to discriminate and identify such sounds. We know from intensive psychoacoustic studies with humans using both simple and complex stimuli, including music and speech, that hearing involves more than just the detection of sound (Miller 1974). In the case of human speech, it is one thing to detect a speech sound in a background noise and quite another to comprehend what is being said. The ability to distinguish whether a sound is different from another requires a higher (better) signal-to-noise ratio than simple detection (Miller et al. 1951). Actual comprehension of speech requires even higher signal-to-noise ratios (Miller et al. 1951). Thus, by analogy, the accurate perception by birds of vocal signals in a noisy background might involve several stages. Initially, a bird must be able to detect songs, calls, or other biologically relevant sounds against the background noise of its habitat. In this sense, detection might be considered the most elementary stage in the perception process (Dooling et al. 2000), and it precedes the problem of discriminating one acoustic signal from another. For a bird, likely acoustic discriminations might include distinguishing conspecific from heterospecific calls, or discriminating among different exemplars of conspecific calls. Finally, acoustic signals perceived by birds in nature are obviously identified, or recognized, as belonging to a particular class of signals. One example might involve the formation of an acoustic perceptual category for the vocalizations of a given individual versus the vocalizations of all others. Discrimination and identification of calls and songs by birds must certainly require higher signal-to-noise ratios than simple detection. Thus, knowing the effect of environmental noise on all stages of perception (detection, discrimination and identification) may well be critical to understanding the evolutionary pressures that shape the perception of these signals.

A final difficulty in studying acoustic space involves the proper way to characterize the level of complex signals that vary in duration or in amplitude over time. The root mean square (RMS) setting on a sound pressure level meter is often used to approximate the integration of acoustic energy over time by the human auditory system. But even though birds and mammals show similar auditory time constants (Dooling et al. 2000), there is no assurance that this method of estimating signal level is most appropriate for birds. Empirical investigations may show that an instantaneous measure of sound intensity, such as peak sound pressure level, rather than a time-averaged measure such as the RMS level, provides a more appropriate way of characterizing the necessary signal level for a bird listening in a noisy environment. With these experiments we hope to identify the signal and masking noise characteristics, as well as any species' perceptual biases, that bear on the detection and discrimination of natural vocalizations in noise.

In the present study we address the basic question of a bird's ability to detect natural vocalizations, rather than pure tones, in a background of noise. To our knowledge this simple question has received only preliminary testing in birds (e.g. Okanoya & Dooling 1991), and our results will provide the first direct data for estimating detection distances of natural signals. In experiment 1 we determine detection thresholds for two species of laboratory birds, the zebra finch, *Taeniopygia guttata*, and budgerigar, *Melopsittacus undulatus*, on calls from three different species: zebra finch, budgerigar and canary, *Serinus canaria*. In addition to testing for the general issue of species specificity (i.e. whether a particular species' calls are more easily heard in noise by that species than by another), these calls allow us to examine the role that signal bandwidth plays in call detection. We compare our results to thresholds for pure tones designed to mimic the frequency and envelope characteristics of these calls. In this experiment we also examine the effect of overall noise level on call detection. In experiment 2 we explore the effect of noise spectral shape on masking effectiveness. Finally, in experiment 3 we examine the effect of masking noise on discrimination among different call types. We wish to determine whether thresholds for the discrimination of vocal signals are different from those for detection of the same signals in a background noise. The experiments presented here provide a more realistic data set from which to estimate distances over which a bird could communicate effectively. In addition they highlight those characteristics of acoustic communication signals that are important to consider when estimating the distances over which birds can detect and discriminate vocalizations in their natural habitats.

GENERAL METHODS

Subjects

Four zebra finches (2 male, 2 female) and four budgerigars (all male) served as subjects in experiments 1 and 2. Two individuals of each species were subsequently used in experiment 3. Zebra finches were offspring of birds obtained through commercial dealers. Budgerigars were first-generation descendants of wild birds obtained from an Australian flock. Birds were housed in individual cages in a vivarium at the University of Maryland, and kept on a normal light/dark cycle correlated with the season. Yellow millet was used as a reinforcer during experimental sessions, and standard mixed finch or parakeet seed was available during free-feeding times. The diet of the birds was monitored to keep them at about 90% of their free-feeding weight.

Apparatus

We tested birds in a small-animal operant conditioning chamber. The chamber consisted of a wire cage (25 × 25 × 25 cm) mounted in a sound-attenuated booth (Industrial Acoustics Company, Inc., Bronx, New York, U.S.A.). One side of the cage was modified to accommodate a custom-built food hopper and response panel. The response panel consisted of two sensitive microswitches with light-emitting diodes (LEDs) attached. The left microswitch served as an observation key, the right microswitch as a report key. Experimental events were controlled with a Pentium microcomputer. Details of the design and set-up of this apparatus have been described previously (Park et al. 1985; Okanoya & Dooling 1988b; Dooling & Okanoya 1995).

Sound stimuli were played through a KEF 60S speaker mounted in the sound-attenuated booth 40 cm above the bird's head. Noise was generated online with a Tucker-Davis Technologies (TDT) waveform generator module (WG1), and shaped and band-passed (900–8000 kHz) using two TDT programmable filter (PF1) modules in series. Call stimuli were stored digitally using the SIGNAL digital signal processing software (Beeman 1998) and output using a TDT DD1 stereo analogue interface at 20 kHz and low-pass filtered at 8.5 kHz. Noise and calls were passed through programmable attenuaters (TDT PA4 modules), mixed (TDT SM3 module) and sent to a Crown D-75 amplifier and finally to the speaker in the sound-attenuated booth. Sound stimuli were calibrated using a Larson-Davis System 824 sound level meter (A-scale, fast response) with a half-inch (1.27-cm) microphone placed in the position in the chamber normally occupied by the bird's head.

Procedure

For experiments 1 and 2, we trained birds to peck the left LED (observation key) repeatedly when they did not hear a call against the continuous noise background, and to peck the right LED (report key) upon detection of a digitized call (target stimulus). The first peck on the observation key started a timer with a random interval of 1–6 s. After the expiration of this time interval, the next peck on the observation key resulted in the presentation of a target. A peck on the report key within 2 s of the presentation of a target was defined as a correct response and was rewarded with a 2-s access to food. Trials in which the subject failed to peck at the report key within 2 s of the presentation of a target stimulus were scored as a miss, the trial was ended and a new trial sequence begun.

Each block of 10 trials contained seven target stimuli and three sham trials (during which no target was presented) in random order. The seven targets consisted of the same digitized call presented at seven different intensity levels in steps of 5 dB. A peck at the report key during a sham trial was scored as a false alarm, and was punished with a 5-s time-out period during which all lights in the test chamber were extinguished. A failure to peck at the report key during a sham trial (the appropriate response) was scored as a correct rejection, at which point the trial was automatically ended and a new trial begun.

We estimated the birds' thresholds using the method of constant stimuli (Gulick et al. 1989; Dooling & Okanoya 1995). To provide the most valid and unbiased comparison of hearing sensitivity across conditions and across species, we calculated thresholds from the psychometric function as the sound pressure level corresponding to a signal detection index for a yes/no task, d', of 2.0 (Gescheider 1985; Dooling & Okanoya 1995). Birds were tested in 100-trial sessions once or twice each day (test sessions in which a bird's false alarm rate exceeded 20% were excluded from analysis). Thresholds were reached when birds showed no further improvement, defined as two successive 100-trial blocks in which the threshold was within ± one-third of the step size. Typically, this required 500–600 trials per bird. These final two sessions were averaged for our threshold estimate. Replicate sessions with familiar stimuli later in these experiments verified that thresholds did not improve beyond 500–600 trials regardless of a subject's familiarity with the stimulus.

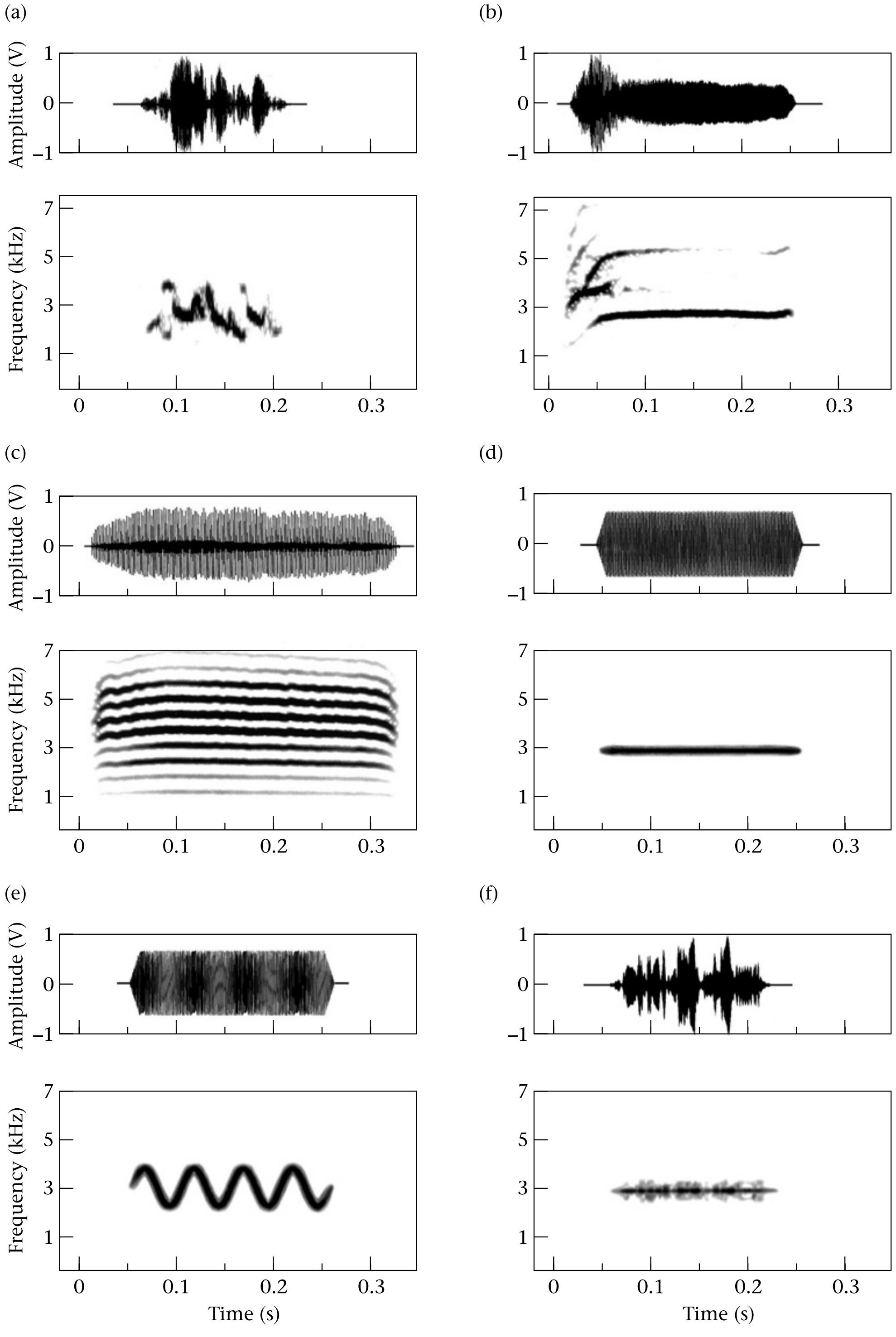

Figure 1. Time waveform and spectrogram from representative examples of (a) a budgerigar contact call, (b) a canary contact call, (c) a female zebra finch contact call, (d) an unmodulated, constant-envelope pure tone at 2860 Hz, (e) a sinusoidally frequency-modulated tone (frequency range 2–4 kHz) and (f) an unmodulated 2860-Hz tone with superimposed amplitude envelope from an original budgerigar test stimulus.

Stimuli

Target stimuli consisted of contact calls of three species: budgerigars, canaries and zebra finches (see Fig. 1 for a representative call of each). We recorded one exemplar of each call from four different individuals of each species. We used calls of three males and one female in the case of budgerigars, and calls from four males in the case of canaries. For zebra finches, in which male and female contact calls differ, we used female contact calls (or ‘long calls') (Zann 1996). Individuals from which calls were recorded were not used as subjects in this study. Canary calls were included in the study as stimuli because they are intermediate in acoustic structure between budgerigar calls and zebra finch calls (e.g. they are closer in bandwidth to budgerigar calls but relatively unmodulated in amplitude or frequency like zebra finch calls). Call durations varied from 146.3 ± 8.9 ms for budgerigars, to 216.3 ± 11.6 for canaries, to 282.0 ± 22.5 for zebra finches ($\bar{X}$ ± SE). Variation in duration in these experiments is not expected to greatly influence thresholds because temporal summation and temporal integration functions for small birds show that thresholds change very little for durations beyond 150 ms (Dooling 1979; Dooling & Searcy 1985). We normalized call levels within the presentation chamber to a standard amplitude using the 'fast' setting on a Larson-Davis System 824 sound level meter, which uses a detector having a time constant of 125 ms. We took an average measure of the maximum sound pressure level recorded for each call using this fast time constant and adjusted the level of these calls so that they were all presented at the same maximum root mean square (RMS) level in the test chamber using this time constant.

Masking Noise

In all of these experiments, the masking noise was band-limited between 900 and 8000 Hz. The noise was digitally 'flattened' (approaching equal energy at all frequencies to within ± 5 dB) by measuring the continuous noise spectrum in the operant chamber, inverting the resultant spectrum, and adding these values to the original noise using a TDT PF1 filter. For experiments 1 and 2, noise was presented at a spectrum level (per cycle energy distribution) of 11.5, 21.5 or 31.5 dB (depending on the experiment), corresponding to overall noise levels of 50, 60 and 70 dB SPL, respectively (measured with the A-weighting of the sound level meter). For experiment 3, band-limited noise was presented at a range of spectrum levels from 23.5 to 35.5 dB (overall noise levels of 62–74 dB SPL).

EXPERIMENT 1

In experiment 1 we determined thresholds for the detection of conspecific and heterospecific calls in the presence of a broadband masking noise. In addition, we measured detection thresholds for an unmodulated 2860-Hz tone and tones designed to simulate the frequency modulation (FM) and amplitude modulation (AM) of budgerigar calls. Budgerigar calls are strongly modulated in both frequency and amplitude whereas canary calls and zebra finch calls show comparatively little FM or AM. In a subset of tests, we evaluated the effect of masking noise level on call detection thresholds. Data for masked tone thresholds show that signal-to-noise levels remain constant over a broad range of overall background noise levels (Fay 1988; Dooling et al. 2000). Our aim with these tests was to determine whether signal-to-noise thresholds for conspecific and heterospecific calls also remain constant over a range of background noise levels.

Methods

Stimuli

The conspecific and heterospecific calls described above were used as stimuli. In addition, we used a pure tone at 2860 Hz with a constant envelope (Fig. 1d) and synthetic tones that mimicked the FM and AM of typical budgerigar contact calls. Our FM tone stimulus consisted of a 200-ms tone centred at 3000 Hz, with sinusoidal modulation between 2000 and 4000 Hz (corresponding generally to the frequency span and number of modulations in a typical budgerigar call), but with a flat amplitude envelope (Fig. 1e). Our AM tone stimuli consisted of a 2860-Hz tone with superimposed amplitude envelopes taken from each of the four budgerigar calls used in the experiment. We tested each subject of the two species with a different AM tone. An example is given in Fig. 1f.

Masking noise

The masking noise was presented continuously, flattened using a TDT PF1 filter module, and band-limited between 900 and 8000 Hz with a spectrum level, or per cycle energy distribution, of 21.5 dB (overall level of 60 dB SPL) as described above. In a subset of tests, noise was presented at three different spectrum levels of 11.5, 21.5 and 31.5 dB (corresponding to overall noise levels of 50, 60 and 70 dB SPL, respectively).

Procedure

Each bird was tested on all 12 call stimuli (each in a different test session) in random order. Subsequent to call detection tests, birds were tested on 2860-Hz tones, FM tones and AM tones in random order, also in different test sessions. We used the average of thresholds across each species' call type for each individual in our comparison of the budgerigar calls, canary calls and zebra finch calls, and compared these with the average thresholds for different types of tones. We used a two-way repeated measures ANOVA (with stimulus type as the repeated measure and test species as the independent factor) to test for significant differences across stimulus types.

Each bird was also tested at different noise levels in random order. In this case, birds were tested on only three calls, one from each species stimulus type (budgerigar, canary, zebra finch), such that subjects within a species received a different call from each set. For each bird, we averaged thresholds from all three call stimulus types for comparison across noise levels. Thresholds were converted to signal-to-noise ratio (threshold level minus spectrum level of the noise) and tested using a two-way repeated measures ANOVA (with noise level as the repeated measure and test species as the independent factor).

Results and Discussion

Thresholds were defined as the SPL corresponding to a performance level equal to a *d′* of 2.0. For both

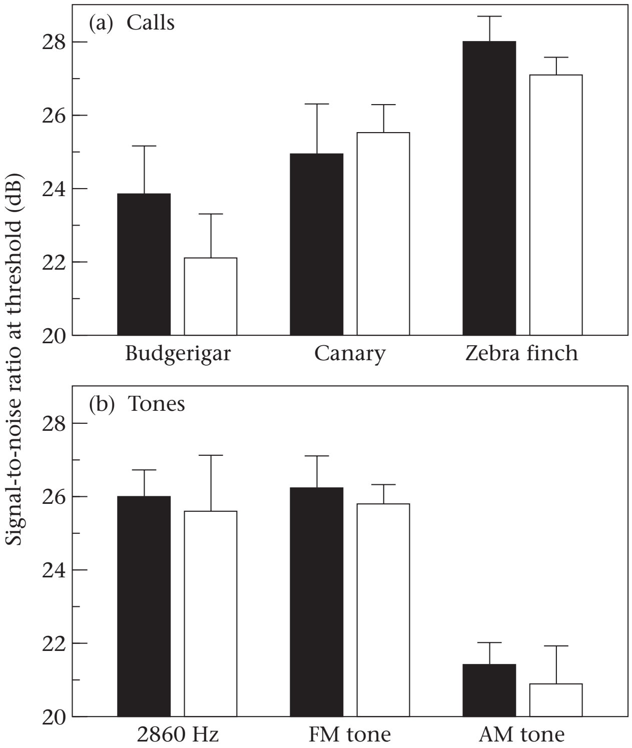

Figure 2. Average budgerigar and zebra finch masked thresholds, expressed as signal-to-noise ratio, for call detection and tone detection in 60 dB (overall SPL) broadband, flat noise. Thresholds are shown for (a) budgerigar, canary and zebra finch calls and are compared with results for (b) an unmodulated pure tone at 2860 Hz, a sinusoidally frequency-modulated tone with constant envelope and an unmodulated 2860-Hz tone with superimposed budgerigar call envelope. ■: Budgerigars; □: zebra finches (*N*=4 birds/bar).

budgerigars and zebra finches, the calls of budgerigars were easiest to detect against a broadband noise background, followed by canary calls, followed in turn by zebra finch calls (Fig. 2). Thus, we found no evidence of a species-specific advantage in ability to detect conspecific calls in the presence of masking noise. Threshold comparisons with a two-way repeated measures ANOVA were followed by Bonferroni-adjusted, pairwise multiple comparisons to assess specific differences between stimulus thresholds. Thresholds for budgerigar test subjects did not differ from those of zebra finch subjects ($F_{1,6}$=1.57, NS). However, differences in detection threshold across all stimulus types were highly significant ($F_{5,30}$=69.22, P<0.001). Post hoc comparisons of data pooled across both test species indicated that thresholds were lowest for AM tones, followed by budgerigar calls (Fig. 2). Thresholds for budgerigar calls in turn were significantly lower than those for canary calls, unmodulated tones and FM tones, which did not differ as a group. Zebra finch call thresholds were highest, and differed significantly from thresholds for all other stimuli except FM tones (Fig. 2).

Using the sound level meter, we also measured the peak sound pressure level for all calls in this experiment. The values for peak sound pressure level minus RMS level are given in Table 1 for all 12 of these calls. In all cases, as expected, the peak sound pressure level was greater than the RMS level. When reported as RMS sound pressure levels, thresholds for call and tone stimuli varied over a range of 20.9–28.0 dB (Fig. 2). When reported as peak sound pressure levels, however, signal-to-noise thresholds across signal types were more similar. In the latter case, thresholds for canary calls and for all tone stimuli were indistinguishable, while thresholds for more complex calls (amplitude-modulated budgerigar calls and broadband zebra finch calls) were somewhat higher ($F_{5,30}$=11.92, P<0.001) (Fig. 3). Furthermore, a comparison of calls within each species' type showed similar differences between peak and RMS measures. For example, the difference between peak level and RMS level of canary call 4 was much less than for the other canary calls (Table 1), and as expected, thresholds for this call

Table 1. Peak level minus RMS level (maximum A-weighted RMS level with a time constant of 125 ms) for stimuli in experiments 1–4

Call type	Call 1	Call 2	Call 3	Call 4
Budgerigar	11.9	14.0	12.9	14.1
Canary	10.0	7.8	10.0	5.6
Zebra finch	8.7	8.3	8.2	10.3

RMS: Root mean square.

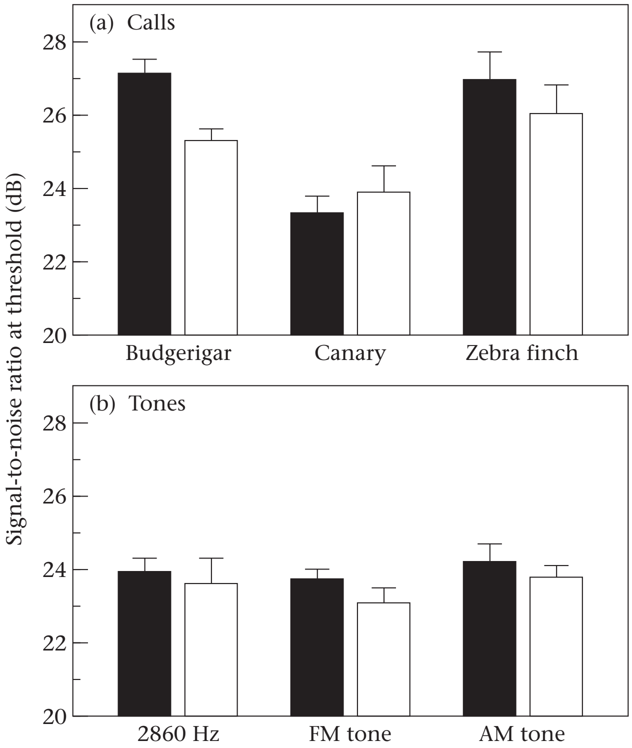

Figure 3. Average budgerigar and zebra finch masked thresholds, expressed as signal-to-noise ratio, for call detection and tone detection in 60 dB (overall SPL) broadband, flat noise. Here thresholds were adjusted by the difference between signal peak level and RMS level. Resulting values indicate detection thresholds that would result if signals had been adjusted by peak level rather than by RMS level. Thresholds are shown for the same stimuli as in Fig. 2. ■: Budgerigars; □: zebra finches (*N*=4 birds/bar).

were significantly higher (worse) than those for the other calls in this set (repeated measures ANOVA: $F_{3,21}=8.79$, $P<0.001$).

When reported in terms of signal-to-noise ratios, average thresholds across species and across call types were 26.6 ± 1.3 dB ($\bar{X} \pm SE$) at a noise spectrum level of 11.5 dB, 25.3 ± 1.3 dB at a noise spectrum level of 21.5 dB, and 26.4 ± 1.6 dB at a noise spectrum level of 31.5 dB. There was no difference in signal-to-noise ratios, at masked threshold, at different background noise levels ($F_{2,12}=3.23$, NS). Again, budgerigar thresholds were not significantly different from zebra finch thresholds ($F_{1,6}=0.57$, NS). We conclude that call masking is independent of noise level, at least over this 20-dB range of background noise. This result for the detection of calls at different masker levels is not unexpected given the independence of critical ratio and masking noise level over a similar overall range in birds (Saunders & Pallone 1980; Okanoya & Dooling 1985, 1987, 1988a) and mammals (Watson 1963; Gourevitch 1965; Johnson 1968; Ehret 1975; Halpern & Dallos 1986).

In summary, there were no species-specific differences in detection threshold. Thresholds increased as frequency bandwidth of the stimulus increased. Thresholds for call detection increased monotonically with the level of background masking noise. When call thresholds were reported as peak sound pressure levels rather than RMS sound pressure levels, differences in detection thresholds across stimuli were reduced, suggesting that peak amplitude may provide a more generally similar, and therefore a more reliably comparable, measure for estimating detection ability across different species for different types of complex calls in noise.

EXPERIMENT 2

In experiment 2 we examined the effect of masking noise type (spectral shape) on call detection. Previous results in a wide range of species have shown that noise energy near the frequency region of the signal contributes more to the masking threshold than does noise energy at spectral regions more remote from the signal (see for example, Fay 1988, for review). We compared thresholds in continuous flat-spectrum noise with thresholds in a continuous traffic-spectrum noise. Traffic noise is weighted towards lower frequencies (<1400 Hz) and is similar in this respect to noise in temperate forests (Klump 1996) and temperate grasslands (Ryan & Brenowitz 1985).

Methods

Stimuli

Test sounds in this experiment were the same call stimuli used in experiment 1. We tested subjects on three calls, one exemplar from each set of call stimuli (budgerigar, canary and zebra finch), such that each subject within a species received a different exemplar from the other individuals of that species. Exemplar assignments to specific subjects therefore were made at random without replacement.

Masking noise

The traffic masking noise was created from the flat noise used in experiment 1. We shaped the noise using a TDT PF1 digital filtering module to coincide with published spectra from studies of traffic noise on busy highways. An average spectral shape was created with data from several studies of traffic noise (see Warring 1972; Cunniff 1977; Bishop & Schomer 1991; Bowlby 1991; Awbrey et al. 1995). This noise was then band-passed between 900 and 8000 Hz using a TDT PF1 module, attenuated to a 70-dB SPL overall level using a TDT PA4 module, and mixed with the call stimuli. Above 1400 Hz, as measured in our acoustic chamber, traffic noise decreased in frequency linearly at a rate of − 2.87 dB/kHz ($r^2=0.93$). When equated for the same overall noise level, the noise levels in different one-third octave bands across the spectrum were not equivalent for the two noise types. There was more energy in the one-third octave bands at lower frequencies for traffic noise compared to flat noise.

Procedure

We measured detection thresholds for call stimuli in a background of noise shaped to match a traffic spectrum. As in the noise level tests of experiment 1, we averaged thresholds from all three call stimulus types for comparison across noise types. We compared average call detection thresholds in traffic noise with average thresholds in broadband noise at 70 dB SPL from the previous experiment. Thresholds were tested using a two-way repeated measures ANOVA (with noise type as the repeated measure and test species as the independent factor).

Results and Discussion

As expected, for the same overall noise level, thresholds were lower for calls in noise shaped to simulate a traffic spectrum than in broadband flat noise (Fig. 4a). That is, it was more difficult to detect a signal against a background of flat noise than against a background of traffic-spectrum noise of equivalent overall dB level. Differences in call detection thresholds for the two noise types were highly significant ($F_{1,6}=119.25$, $P<0.001$). As in previous experiments, budgerigar thresholds did not differ from those for zebra finches ($F_{1,6}=0.001$, NS).

We calculated signal-to-noise ratios using the spectrum level of the one-third octave band of noise at the spectral region containing the peak energy for each call, rather than overall noise level (Fig. 4b). Signal-to-noise ratios at threshold calculated in this way showed no difference between the two background noise types (flat spectrum versus traffic spectrum) ($F_{1,6}=4.79$, NS), or between subject species ($F_{1,6}=0.001$, NS). Thus, when considering only the noise level in the spectral region of the peak signal energy, differences in call detection between the noise spectral shapes were eliminated. Otherwise said, the signal was more effectively masked by noise energy in the spectral region of the signal than at spectral regions remote from the signal.

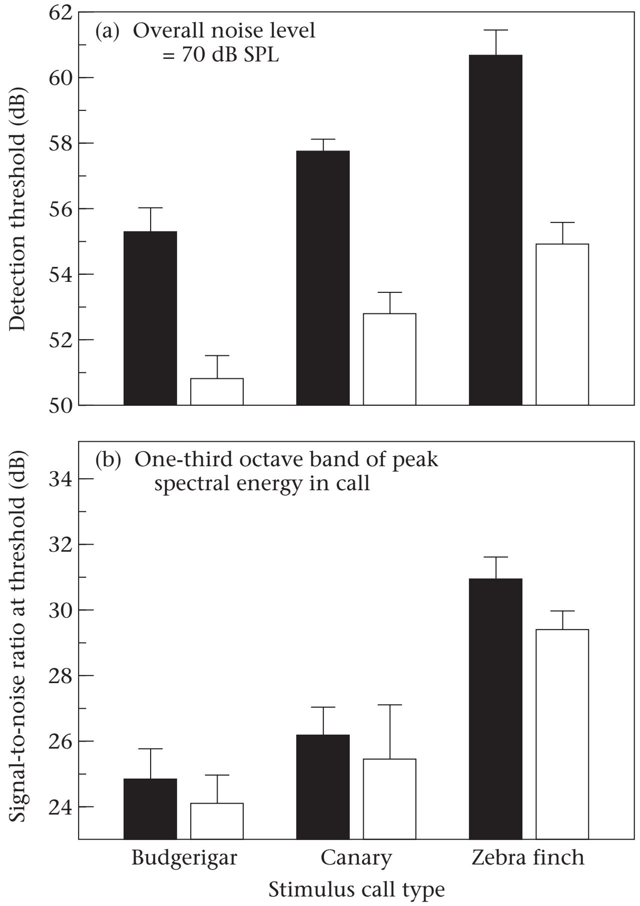

Figure 4. Budgerigar and zebra finch masked thresholds, expressed as the (a) threshold in overall noise level of 70 dB SPL and (b) signal-to-noise ratio at threshold using the spectrum level of noise in the one-third octave band of maximum signal energy. The one-third octave band of maximum signal energy ranged from 2500 to 6300 Hz (centre frequencies). ■: Thresholds in broadband, flat noise; □: thresholds in noise having a traffic spectrum (*N*=8 birds/bar).

EXPERIMENT 3

In experiment 3 we measured the effect of a broadband, flat masking noise on the discrimination of contact calls. We compared call discrimination thresholds with detection thresholds at equivalent performance levels to determine whether discrimination between calls requires higher signal-to-noise ratios than call detection.

Methods

Stimuli

The stimuli for the experiment were the budgerigar and zebra finch calls used in the previous detection experiments. All call stimuli in this experiment were presented at 60 dB SPL.

Masking noise

Noise was flattened and then band-limited between 900 and 8000 Hz. Noise levels ranged from 62 to 74 dB SPL (spectrum level of 23.5–35.5 dB) in 2-dB steps.

Procedure

In this task, instead of presenting a call against a background of noise and requiring subjects to detect it, subjects had to discriminate a repeating background call from a target stimulus consisting of another call. Stimuli were presented at a rate of two calls/s. Birds were trained to peck the observation key repeatedly until a target stimulus alternated with the background stimulus. Target and background calls for any given session were always from the same species (i.e. budgerigar calls were discriminated from other budgerigar calls, and zebra finch calls from other zebra finch calls). Budgerigars and zebra finches were initially tested on their ability to discriminate both within a set of four conspecific calls and within a set of four heterospecific calls in the presence of masking noise at an overall level of 60 dB SPL. In each set, one call was used as a repeating background. Another call from the same species, selected at random, was then alternated with this call during target presentations. These initial tests revealed two pairs of budgerigar calls that both budgerigar and zebra finch subjects could not correctly discriminate at levels higher than a of *d′* of 2.0. We excluded these call pairs from further analysis because we were primarily interested in the effect of increased levels of masking noise on discrimination abilities. We performed separate discrimination tests in 50-trial blocks with 12 different background noise levels. Order of blocks (noise level) was randomized for each bird. We interpolated between tested noise levels to estimate the average sound level at which the birds performed at a *d′* of 2.0. We used two budgerigars and two zebra finches as subjects in this experiment. These birds were subjects in the previous experiments.

Results and Discussion

Overall, discrimination thresholds in this experiment were higher than detection thresholds by an average of 3.29 dB. This consistent difference between thresholds for discrimination of calls versus detection of calls suggests that it is more difficult to discriminate among several calls in the presence of masking noise than it is to detect the presence of those same calls in noise. Performance for discrimination between most pairs of calls was close to 100% at high signal-to-noise ratios but dropped as the level of background noise increased. Thresholds for discrimination of calls (when *d′* reached a level of 2.0) ranged from 25.5 to 30.9 dB (signal-to-noise ratio) and were always higher than thresholds for the detection of the same calls (Table 2). Average individual psychometric functions for discrimination of calls are shown in Fig. 5.

As with simple detection of these calls, we found no evidence of a species-specific advantage in threshold for discriminating between conspecific calls in the presence of masking noise. Both budgerigars and zebra finches showed a lower threshold for discriminating between budgerigar calls than between zebra finch calls (Table 2). There was, however, a significant species effect at higher signal-to-noise ratios. A two-way repeated measures ANOVA for species' call type and noise level showed a

Table 2. Comparison of detection thresholds and discrimination thresholds for subjects in experiment 4

	Budgerigar calls		Zebra finch calls	
Subjects	Detection	Discrimination	Detection	Discrimination
Budgerigars				
Subject 1	25.2	25.5	28.3	29.2
Subject 2	22.1	26.4	27.8	30.7
Zebra finches				
Subject 1	21.0	25.8	26.5	28.0
Subject 2	22.4	30.8	27.7	30.9

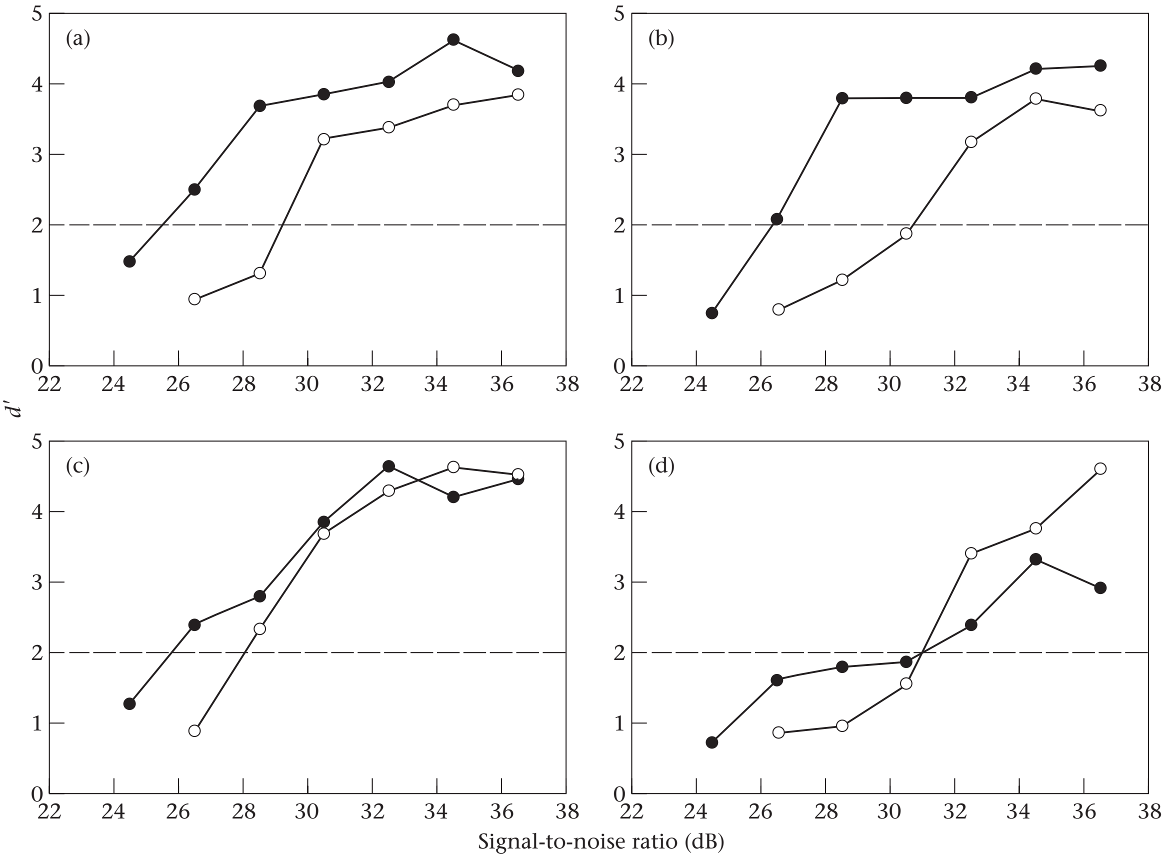

Figure 5. Psychometric functions for discrimination among calls in different levels of broadband, flat noise, expressed as signal-to-noise ratio, for (a) budgerigar subject 1, (b) budgerigar subject 2, (c) zebra finch subject 1 and (d) zebra finch subject 2. ●: Budgerigar calls; ○: zebra finch calls. Dashed horizontal lines indicate a *d′* of 2.0.

significant effect of both call type (subject 1: $F_{1,10}$=18.99, $P<0.01$; subject 2: $F_{1,8}$=21.06, $P<0.01$) and noise level (subject 1: $F_{4,40}$=13.45, $P<0.001$; subject 2: $F_{5,40}$=27.35, $P<0.001$) in budgerigars. In zebra finches, however, only comparisons of threshold across noise levels were significant (subject 1: $F_{5,50}$=48.54, $P<0.001$; subject 2: $F_{5,40}$=18.35, $P<0.001$); differences between call types were not (subject 1: $F_{1,10}$=2.25, NS; subject 2: $F_{1,8}$=0.08, NS). Thus, when calls in noise were presented at levels well above threshold, budgerigars discriminated among budgerigar contact calls more accurately than they did among zebra finch calls (Fig. 5a, b). However, at least one zebra finch in this experiment did not discriminate zebra finch calls more accurately than budgerigar calls (Fig. 5c), while the other did so only at the highest signal-to-noise levels (Fig. 5d).

GENERAL DISCUSSION

The aim of these experiments was to identify the acoustic features and species-specific variables influencing a bird's ability to detect and discriminate vocalizations against a background of noise. Data from these experiments allow us to make initial predictions regarding the likely active space of conspecific and heterospecific calls given known values of standard acoustic parameters that may be easily measured in the field. In general, our results show an overall similarity among divergent bird taxa (parrots and songbirds) in their ability to detect and discriminate among a range of vocalization types in a noise background (i.e. data for budgerigars and zebra finches follow similar patterns across different species' calls). Species calls used in this study were chosen on the basis of their acoustic diversity (e.g. bandwidth), and their similar function across test species (e.g. all are 'contact' calls). While the distances over which these calls are typically used in the wild varies, the narrowband calls of budgerigars and canaries are similar in their spectral and temporal characteristics to the advertising songs of many oscines, and may serve as useful general models for vocal detection and discrimination. Our results suggest that birds are attending to general acoustic properties of calls rather than relying on special abilities to detect and discriminate conspecific versus heterospecific call characteristics, at least at threshold levels. Species-specific abilities may be demonstrable under certain conditions in birds, for instance when discriminating conspecific versus heterospecific calls above threshold, or when classifying conspecific versus heterospecific calls more accurately and quickly (Dooling et al. 1992). But it appears that general acoustic features are most likely involved in the detection and discrimination of acoustic communication signals in noise.

Call Characteristics Affecting Detection Threshold

The overall level of a sound such as a bird vocalization is typically measured in the free field using a sound level meter, perhaps using an A-weighting function to reduce the influence of low-frequency energy. Our results suggest ways that this measure may be interpreted so as to be most relevant to the problem of acoustic communication by birds in the field. We show that thresholds for conspecific and heterospecific signals described by their overall RMS level as expressed in dB SPL are influenced by both signal bandwidth and amplitude modulation, as well as several other considerations.

If the total energy in a signal is concentrated in a narrow frequency region approximating that of an unmodulated pure tone, thresholds are likely to be lower than if the total energy is spread across a broader frequency range. Thus, canary calls show thresholds like pure tones and zebra finch calls, having much broader bandwidth (Fig. 1), have higher thresholds (Fig. 2a). If signal bandwidth were the only determining characteristic for detection thresholds, however, we would expect to find that adding frequency modulation (FM) would make tone thresholds more like those of broadband calls. Adding FM to tones to simulate the FM in budgerigar contact calls did not change their detection thresholds significantly, while imposing amplitude envelopes from the budgerigar calls on pure tones, for instance, did change the detectability of these tones in noise (Fig. 2b).

Amplitude modulation improves the detectability of a signal in noise. Given the same overall sound pressure level, if the vocalization has a peaky (not smooth) waveform envelope, the call will be more detectable than if it has a smooth envelope. Thus, budgerigar calls and AM tones had the lowest thresholds among our stimuli (Fig. 2). Interestingly, tones with budgerigar-like AM gave lower thresholds than budgerigar calls (i.e. lower than tones, canary calls and FM tones). This result may reflect the fact that budgerigar calls, although relatively tonal, still have a broader bandwidth than a pure tone, spreading beyond one critical bandwidth of the budgerigar auditory system (Dooling et al. 2000). FM in budgerigar calls is often more rapid than the sinusoidal modulation of our FM tones (Fig. 1), effectively giving them a greater bandwidth over short timescales.

In summary, peak sound pressure levels (as recorded on a sound level meter), rather than RMS sound pressure levels, lead to more similar estimates of thresholds across a diversity of song- and call-like sounds. When reported as peak SPL rather than RMS SPL, thresholds were statistically indistinguishable for canary calls and all tone stimuli (Fig. 3). Only acoustically more complex sounds such as budgerigar and zebra finch calls had different thresholds. In the case of zebra finch calls, this is probably due to the spread of acoustic energy across more than one frequency band. With budgerigar calls this may be the case as well, given the rapid amplitude modulations that occur in calls of this species.

Effect of Noise Level and Spectrum

Signal-to-noise ratio at threshold for call detection was constant over a wide range of background noise levels for both budgerigars and zebra finches. Our result is not surprising as similar results were obtained for a variety of other birds and mammals tested on tones in noise (Fay 1988). This linear increase in signal detection threshold with background noise level has implications for the active acoustic space of a bird in its natural environment. If spherical spreading is the primary source of signal attenuation, signal level should decrease by at least 6 dB with each doubling of distance from the source (Wiley & Richards 1982). If background noise is relatively uniform and signal level is fixed at the source, the detection distance of a signaller should be predictable if the threshold for that signal type is known.

One complicating factor is whether birds have the ability to alter signal source level with variation in noise level. There is little direct data concerning the ability of territorial songbirds to produce song of variable absolute amplitude in the field. The ability to modify call amplitude under different noise conditions, however, has been demonstrated in the laboratory in several birds, mammals and anuran amphibians (Potash 1972; Sinnott et al. 1975; Lopez et al. 1988; Cynx et al. 1998; Manabe et al. 1998). If a bird is capable of making adjustments in vocal amplitude under natural conditions, it could offset to some extent the detrimental effects of ambient noise level.

Effect of Noise Spectral Shape

We compared detection thresholds in traffic-spectrum noise with those in flat-spectrum noise to examine how different types of noise might affect detection thresholds. We would predict for a given overall level that noise shaped like a traffic spectrum should produce less masking of bird vocalizations than broadband noise. Our results suggest that the effect of different noise types is a function of the amount of masking noise in the spectral band having the greatest signal-to-noise ratio. This is often, although not always, the frequency region of peak call energy in the signal. We used one-third octave bands in this instance because they provide a reasonable approximation to the size of auditory filter bandwidths in humans and probably also in most birds (but see Langemann et al. 1995), and provide a standard bandwidth for making comparisons of signal-to-noise ratio at threshold across calls (Saunders et al. 1978; Dooling & Searcy 1979; Langemann et al. 1995; Marean et al. 1998). As expected, traffic noise resulted in less masking of vocalizations than did a flat-spectrum noise of the same overall sound pressure level. A greater proportion of the energy in traffic noise is in channels lower than those occupied by the signal. When we examined signal-to-noise ratios within the one-third octave bands of maximum power in each signal, differences between signal-to-noise ratio at threshold for the two noise types disappeared. We conclude that when predicting the masking effect of a continuous noise, the specific spectral shape of the noise is less important than the signal-to-noise level within the frequency band of maximum signal power.

Call Discrimination versus Detection

We provide evidence that for a given level of noise, call discrimination is more difficult than call detection. Discrimination thresholds were higher than detection thresholds for both subject species on all stimulus comparisons. This result was expected both from anecdotal evidence of humans listening to speech in noise and from more formal studies of speech perception (Miller 1974). Signal discrimination is obviously important in the social behaviour of many species of birds and other animals using acoustic signals, and distinctions between discrimination abilities and detection abilities in noise are not limited to humans and birds. Anuran amphibians, for example, rely on the ability to make discriminations between different male calls in a noisy background (Gerhardt 1989, 1994), and such discrimination thresholds are likely to be higher than detection thresholds as well (Wollerman & Wiley 2002).

Marten & Marler (1977) and Brenowitz (1982) define ‘active space’ as the maximum distance at which a signal can be detected against a background of noise. From the perspective of a communication signal’s functional utility, an effective communication distance might more accurately be defined in terms of the distance over which its ‘meaning’ can be transmitted. In some solitary or territorial species, detection thresholds for signals may be sufficient for estimating effective communication distances. In most species, particularly very social ones, discrimination of specific signal exemplars is paramount, and call discrimination thresholds or call recognition thresholds are likely to provide a more useful prediction of the functional active space of a signal than detection thresholds.

Recognizing individuals or classes of conspecifics (males versus females, neighbours versus strangers, etc.) by differences in their vocalizations implies an ability to discriminate reliably between calls. In nature, such discrimination often must be accomplished in a background of noise generated predominantly by the vocalizations of large numbers of conspecifics, as in a breeding colony or a mating assemblage. While such noise is clearly in the same frequency channel as the calls that are being detected, there may be special processes by which discrimination abilities are improved. The ‘cocktail-party’ effect in human speech (Cherry 1966) for example, is a well-known mechanism by which the discrimination of familiar speech sounds is enhanced in a background of speech-generated noise. While there are few studies demonstrating similar abilities in birds (see Aubin & Jouventin 1998), it is possible that mechanisms for enhancing the ability to discriminate familiar signals in certain types of noise may exist for other species as well.

Call Discrimination: Species Specializations

At threshold, we found no evidence for species specializations in call discrimination. Both zebra finches and budgerigars had lower call discrimination thresholds for budgerigar calls than for zebra finch calls. This result suggests that general acoustic characteristics of these calls are the principal features used in discriminating among exemplars in high levels of background noise. As in call detection, differences between peak and RMS values for our calls due to amplitude modulation provide a likely explanation for the lower budgerigar call thresholds. In another context, Medvin et al. (1993) demonstrated that cliff swallow, *Hirundo pyrrhonota*, calls are more individually distinct and have a greater capacity for carrying information than calls of barn swallows, *H. rustica*. When cliff and barn swallows were tested on their ability to discriminate a set of conspecific and heterospecific calls, both species had less difficulty discriminating among cliff swallow calls (Beecher et al. 1989). Here again, more general mechanisms of auditory perceptual ability are evident.

Under certain circumstances, the perceived similarity of calls and subsequent degree of difficulty in discriminating among them also may depend on the species producing and perceiving the call, however. Dooling et al. (1992) tested the ability of budgerigars, canaries and zebra finches to discriminate between calls of each of the three species using response latency as a measure. In this case, each species was best able to discriminate among its own species’ calls, suggesting that special perceptual abilities might exist for discriminating among conspecific calls in these species. Our results here further support the possibility for special perceptual abilities in budgerigars. At noise levels above threshold, budgerigars performed best on conspecific versus heterospecific call discriminations (Fig. 5). Our data are less supportive of such a conclusion about species specializations in zebra finches. Benney & Braaten (2000) found that zebra finches performed more quickly when identifying specific songs among mixtures of songs from several species if target songs were conspecific. However, using single exemplars in noise at levels above threshold, we found a possible species-specific advantage in accuracy for only one of two zebra finches when discriminating among zebra finch calls versus budgerigar calls (Fig. 5).

Implications for Communicating in a Natural Habitat

Estimating the effective communication distance of acoustic communication signals in the field is complicated by the many factors that can contribute to the masking of these signals. Our experiments address only the simplest case of call detection and discrimination with a continuous background noise. Noise in natural environments is rarely continuous, for instance (Klump 1996), and signallers may take advantage of gaps in noise to improve signal-to-noise ratio (Ficken et al. 1974; Narins & Zelick 1988; Popp 1989; Narins 1992; Schwartz 1993; Greenfield 1994; Grafe 1996). Birds also may use amplitude fluctuations affecting both signals and noise, considerable in some natural environments (Wiley & Richards 1982), to enhance their ability to detect signals in noise. Such spectrotemporal, or comodulation, masking release (Klump & Langemann 1995) can improve signal-to-noise ratios in birds by 10 dB or more (Klump & Langemann 1995; Dent et al. 1997). Finally, the spatial separation of signal and noise source may be used to improve signal detection. Spatial release from masking has been well studied in humans (Saberi et al. 1991), and has been shown to similarly enhance signal detection abilities in green treefrogs, *Hyla cinerea* (Schwartz & Gerhardt 1989), budgerigars (Dent et al. 1997), and ferrets, *Mustella putorius* (Hine et al. 1994). While our thresholds present something of an ideal case, they go beyond traditional masking studies that use tones and white noise in providing data to estimate minimum distances over which calls can be transmitted in noise.

An important caveat when considering the potential improvements in signal-to-noise ratio suggested above involves the effects of the habitat on the signal. Calls are altered when travelling through the habitat, and this acoustic degradation may change the characteristics important for evaluating detectability and discriminability (Wiley & Richards 1982; Dabelsteen et al. 1993; Holland et al. 1998; Naguib et al. 2000). Signal degradation in the form of high-frequency attenuation, reverberation and 'blurring' of amplitude and frequency patterns will alter a call's temporal fine structure, affecting the 'peakiness' of the waveform (Wiley & Richards 1982; Dabelsteen et al. 1993). Thus, using an undegraded call in masked detection and discrimination tests may provide a less accurate estimate of actual effective communication distance than a call re-recorded at biologically relevant distances in appropriate habitats.

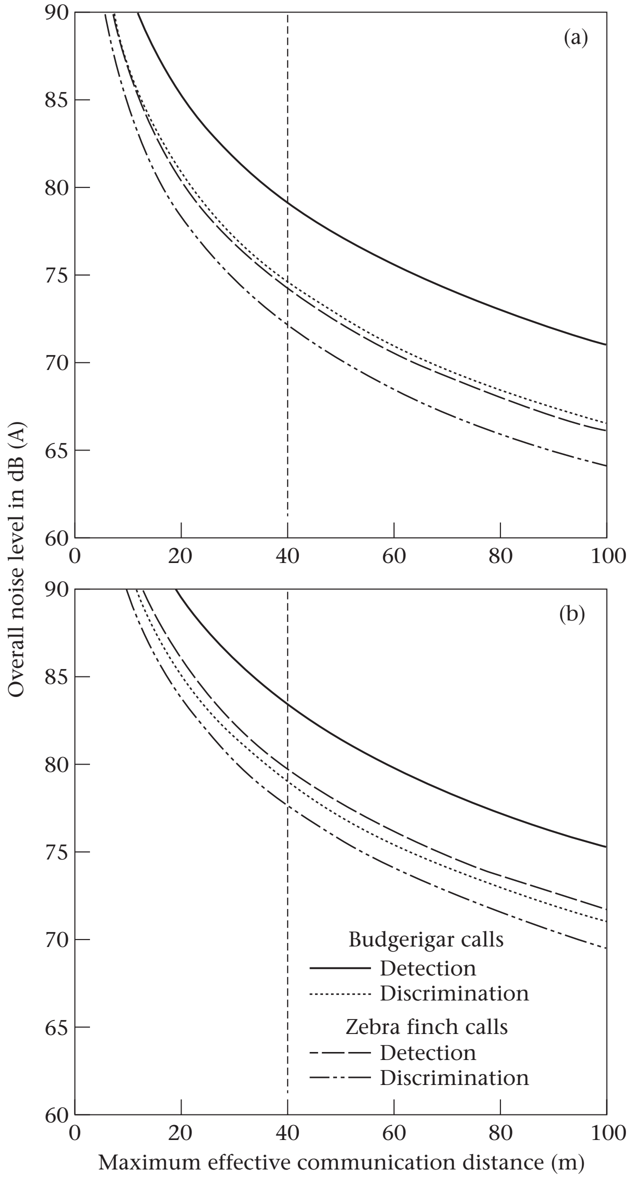

Figure 6. Theoretical maximum communication distances based on detection and discrimination thresholds for budgerigar and zebra finch calls in (a) broadband flat noise and (b) traffic-spectrum noise. Curves illustrate distances based on detection thresholds and discrimination thresholds, and assume excess attenuation of 5 dB/100 m and a source intensity of 95 dB SPL measured using the maximum fast (125-ms RMS) setting on a sound level meter. Background noise is given in overall dB SPL (A) for both types of noise. The vertical dashed line represents a distance of 40 m. In most cases, discrimination threshold distances (dotted lines) probably represent the maximum limit for communication distances (or 'active space') for a given call type.

Estimating Communication Distances: a Simple Example

We generated a series of curves to describe maximum effective communication distances under two noise conditions based on our thresholds for budgerigar and zebra finch calls (Fig. 6). The theoretical maximum communication distance (d_{mc}) can be estimated by solving the following equation adopted from Marten & Marler (1977) and Dooling (1982):

$$\mathrm{Drop} = 20 \times \log\left(\frac{d_{\mathrm{mc}}}{d_{\mathrm{o}}} + \frac{\mathrm{EA} \times d_{\mathrm{mc}}}{100}\right),$$

where drop is the amount of signal attenuation from source intensity to that at threshold, d_{mc} is the maximum communication distance, d_{o} is the distance at which source intensity is measured, and EA is the amount of excess attenuation (or constant attenuation not due to spherical spreading). For the curves represented in Fig. 6 we used a source intensity level of 95 dB at 1 m and an excess attenuation of 5 dB/100 m. These values fall within the range of those measured in the field, but are on the high end for source intensity (Brackenbury 1979) and the low end for excess attenuation (Marten & Marler 1977; Brenowitz 1982) (see Dooling 1982 for relationships to other source intensities and values for excess attenuation). Thus, our curves provide an estimate of maximum communication distance under fairly good conditions from the perspective of a receiver. While we recommend using peak measures for estimating detection and discrimination thresholds given our results in experiment 1, signal-to-noise thresholds based on RMS levels are shown here to illustrate the clear differences between different call types (budgerigar versus zebra finch). At RMS source intensities of 95 dB SPL at 1 m, a bird can detect and discriminate budgerigar calls at longer distances than it can zebra finch calls (Fig. 6).

As expected, distances over which signals may be discriminated are shorter than distances at which those same signals may be detected. In the simplest possible case, assuming no excess attenuation, our average difference between detection and discrimination thresholds of 3.29 dB translates to a linear discrimination distance that is 0.685 of the distance at which the same signal may be detected. The dashed vertical line on each graph in Fig. 6 indicates an interindividual communication distance of 40 m. Based on our results, a flat-spectrum noise with an overall level of 75 dB SPL is likely to limit communication ability in a songbird that typically communicates with conspecifics at that distance (Fig. 6a). A traffic-spectrum noise of equal overall sound pressure level may not limit communication in this songbird (Fig. 6b). To evaluate predictions of this model for a particular species, it is clearly necessary to obtain information regarding typical linear communication distances for that species, as well as appropriate song source intensities, song spectra and sound transmission characteristics of typical habitats for that species.

In the wild, making fine distinctions between conspecific or even heterospecific communication signals can provide crucial information to individuals. In humans the ability to make finer distinctions between speech sounds improves steadily with greater signal-to-noise ratios (Miller 1974). Particularly in threatened or sensitive species exposed to increased levels of anthropogenic or other noise sources, the masking of communication signals and its consequences for social behaviour is of concern. While we have shown that several simple acoustic characteristics are likely to provide important information in evaluating the impact of noise on the detection and discrimination of biologically relevant signals, our estimates should be taken as best-case possibilities. Actual effective communication distances are likely to be smaller than those predicted by our simple model given probable higher levels of excess attenuation, degradation of the stimulus, and the likelihood that recognition or identification of a signal, rather than simply detection or discrimination, is necessary for effective communication to take place. Nevertheless, the thresholds we report for most types of tones and vocalizations were remarkably similar when recorded as peak levels. Overall noise levels and at least one noise spectrum used in our study are similar to background noise in some natural habitats (Brenowitz 1982; Ryan & Brenowitz 1985; Robisson 1991; Klump 1996; Aubin & Jouventin 1998). Furthermore, an examination of critical ratio functions for most birds tested thus far show that they lie between those of budgerigars and zebra finches over the range of frequencies in which most vocalizations occur (Fay 1988; Dooling et al. 2000). Given the general uniformity of hearing abilities in birds (Dooling et al. 2000), and a knowledge of the noise and degradation characteristics of a particular habitat, our results provide a good starting point for estimating the likely 'active space' of communication signals in birds.

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