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Transmission Effects on Temporal Structure in the Advertisement Calls of Two Toads, *Bufo woodhousii* and *Bufo valliceps*

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With 2 figures

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Abstract

We measured degradation of temporal structure in the advertisement calls of two species of toads (*Bufo woodhousii* and *B. valliceps*) as a function of transmission distance. Degradation, measured as the ratio of the amplitudes of pulse and interpulse interval, increased with distance and was significantly greater in *B. valliceps* than in *B. woodhousii*. These results are compared to previous reports of neural thresholds for units in the torus semicircularis that are responsive to the interaction of depth and rate of amplitude modulation in *B. woodhousii* and *B. americanus*. We suggest that the degradation of temporal structure that we measured has behavioral and neurophysiological consequences for communication.

Introduction

The ability to attract mates requires the production, transmission and reception of a readily identifiable signal from one sex to the other. In many organisms, especially anurans, insects, and birds, males rely on species-specific acoustic signals to attract females over long distances. Spectral components of these sounds can be important in mate attraction and recognition. Many studies have addressed how the differential attenuation of spectral components of acoustic signals constrains the distance over which effective long-range communication is possible (e.g. MORTON 1975; MARTEN et al. 1977; BRENOWITZ 1983; BOWMAN 1983; RYAN & BRENOWITZ 1985; RYAN 1986, 1988).

Many species of anurans and insects also rely extensively on a signal's temporal structure for mate attraction (e.g. GERHARDT 1974, 1978, 1981; POLLACK

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& Hoy 1979). In North American toads (genus *Bufo*) the variation among species in spectral components of calls is small relative to the variation in temporal components, especially the pulse repetition rate. A number of authors have suggested that these differences in pulse rate are critical for species recognition (e.g. Blair 1958, 1964); for example, female *B. woodhousii* are attracted preferentially to acoustic stimuli pulsed at the species-typical rate (Sullivan & Leek 1987).

In anurans there is a bias in the frequency response of the auditory system toward those frequencies that characterize the conspecific advertisement call (Capranica 1976; Fuzessery 1988). Similarly, recent studies have shown that some components of the auditory system are also biased or tuned to synthetic patterns of amplitude modulation (AM) that correspond to the pulse repetition rate of the conspecific call (Rose & Capranica 1983, 1984; Rose et al. 1985; Walkowiak 1988). The "tuning" of these AM selective units in the torus semicircularis is represented in one of two ways. First, there is variation in spike rate as a function of rate of AM, in which the unit is tuned to the rate of AM that elicits the maximum spike rate. The second estimate of tuning examines neural-threshold response as a function of depth and rate of AM. By definition, the unit is tuned to the rate of AM that elicits a response with the least depth of AM. This latter measure has been used to argue that differences between species in AM tuning are consistent with differences in pulse repetition rates of the species-specific advertisement call (Rose & Capranica 1984).

Temporal structure of signals needs not be preserved during transmission. Due to reflection and diffraction in acoustically complex environments, sound reaches a receiver by multiple pathways and "smearing" of the signal can result (Wiley & Richards 1982). One of the temporal components most affected by this smearing is depth of AM (Richards & Wiley 1980). In the advertisement calls of many toads, this is analogous to a decrease in the ratio of the amplitude of the pulse relative to the amplitude of the interpulse interval. Other factors, such as increased background, will also decrease this amplitude difference. The pulse-repetition rate cannot be decoded unless the animal perceives differences between the amplitudes of the pulse and interpulse interval.

The purpose of our study is to identify patterns of temporal degradation in the calls of two species of toads in which: (1) calls are used to attract mates over long distances; (2) calls differ between species in a variety of temporal parameters, including pulse-repetition rate which is thought to be the primary cue for mate recognition; and, (3) neurophysiological studies suggest that the depth of AM is a critical variable for eliciting response from temporally selective units in the auditory system.

Methods

Naturally recorded calls of an individual male *Bufo woodhousii* and *B. valliceps* were broadcast and rerecorded at two sites near Austin, Texas in August 1986. Both species bred at these sites during the summer months. Site 1 was a rain-formed pool located in an open expanse of Blackland Prairie habitat in southern Williamson County, Texas. This community was dominated by a dense growth of annual plants approximately 0.5 m in height. Site 2 was a rain-formed pool located 10 km to the west

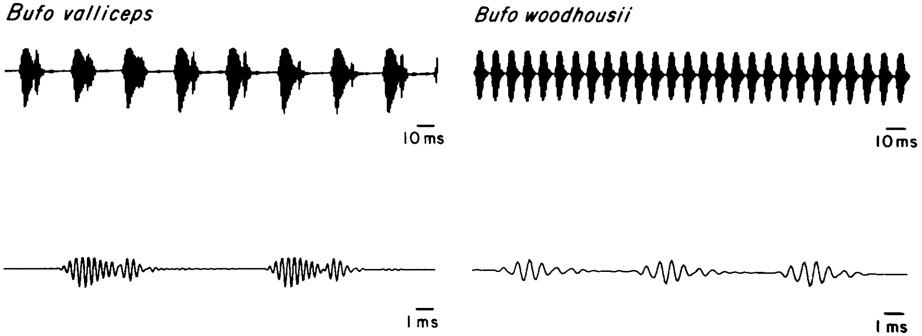

Fig. 1: Oscillograms (time vs amplitude) of an advertisement call of *Bufo woodhousii* and *Bufo valliceps*. The top graph in each pair represents a large number of pulses, while the bottom graph of each pair is an expanded display of several pulses

of site 1 in an open Oak-woodland habitat on the Edwards Plateau also in Williamson County, Texas. This site was also dominated by a dense growth of annual plants approximately 0.5 m tall. At this second site no large perennial plants were located within 2 m of the transmission line used during the experiments. Calls were broadcast from the shoreline away from the pond.

The calls were similar in dominant frequency (*B. woodhousii* = 1.44 kHz; *B. valliceps* = 1.30 kHz). They differed in several temporal aspects. The *B. woodhousii* call had a pulse-repetition rate of ca. 125 Hz, a pulse duration of ca. 5.1 ms, and an interpulse interval of ca. 2.9 ms (Fig. 1). The *B. valliceps* call had a much slower pulse rate of ca. 40 Hz, and a longer pulse duration and interpulse interval, ca. 10.8 ms and ca. 12.8 ms, respectively. The calls were similar in the ratio of the amplitudes of the pulse and interpulse interval, 0.93 for *B. woodhousii* and 0.96 for *B. valliceps*. Our measure of this ratio was $_{\Delta}V = 1 -$ (RMS IPI/RMS P), where $_{\Delta}V$ is the ratio of the amplitudes of the pulse and interpulse interval, RMS P is the root-mean-square amplitude of a single pulse and RMS IPI is the root-mean-square amplitude of the following interpulse interval (Fig. 1). Root-mean-square rather than peak amplitude was used because it is less sensitive to small fluctuations in amplitude.

Calls were broadcast with a Sony TCD-5M tape recorder, a portable amplifier, and a small extension speaker. All calls were broadcast at ground level, where the toads call. Calls were recorded at the following distances from the speaker: 1, 5, 10, 20, 50 and 80 m. The calls were recorded with an Uher 4200 stereo recorder and a Sennheiser ME 80 microphone with a K3U power module. Experiments began at dusk, the time of day when toads usually begin to call. At the beginning of both experiments, temperatures were over 30 °C with little or no detectable wind.

Calls were analyzed on a DATA 6000 digital waveform analyzer at a sampling rate of 10 kHz. The broadcast calls were first digitally stored and were then used as templates for an exact determination of the pulse and interpulse intervals of the recorded calls. Using a template removed error in determining the exact onset and offset of pulses which tended to be smeared in calls recorded at far distances. The RMS amplitude of ten pulses and their following interpulse intervals were determined for each distance. $_{\Delta}V$ was determined from the formula given above.

Table 1: Regression equations of $_{\Delta}V$ as a function of distance (data transformed by arcsine square root)

Species	Site	Equation	R^2	p
Bufo valliceps	1	$Y = 1.01 - .012\ X$	.89	.003
Bufo valliceps	2	$Y = 1.14 - .007\ X$	.87	.002
Bufo woodhousii	1	$Y = 0.82 - .005\ X$	.39	.130
Bufo woodhousii	2	$Y = 1.03 - .005\ X$	.67	.025

The rate of change of ΔV as a function of distance was represented by the slope of the least squares regression. Since ΔV is a ratio, regressions were calculated using the arcsine square root of the mean ΔV at each distance for each species and site. Multivariate analysis of variance was used to compare the mean ΔV among species and sites within each distance; data were transformed by arcsine square root prior to analysis.

Results

For both species at both sites ΔV decreased as a function of distance (Fig. 2). The minimum decrease was 35.4 % (.938 to .584) for *B. woodhousii* at site 2, while the greatest decrease was 81.5 % (.958 to .143) for *B. valliceps* at site 1. The slopes of the regression equations ranged from −.012 to −.005, indicating that (arcsine) ΔV decreased an average of 0.5—1 % for each meter the call was transmitted. The regression of the ΔV on distance was not statistically significant for the *B. woodhousii* calls transmitted at site 1 (Table 1).

We compared the slopes of the regressions to determine how the rate of temporal degradation varied among species and sites. The slopes for *B. woodhousii* calls at the two sites did not differ significantly ($F = .003$, $p = .96$; Table 1), while the slopes for the *B. valliceps* calls were marginally different among sites ($F = 5.02$, $p = .049$). However, when the data from each site were combined for each species and the regressions compared, there was a significant difference in the slopes of the regressions between species ($F = 11.0$, $p < .001$).

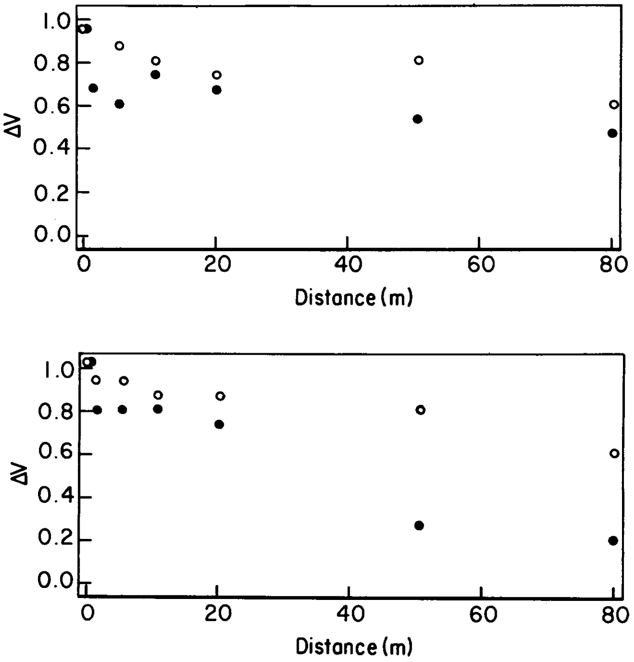

Fig. 2: The change in ΔV as a function of distance for *Bufo woodhousii* (top) and *B. valliceps* (bottom). Closed circles: data from site 1, open circles: data from site 2

Table 2: Results of a multiple analysis of variance (F statistic and associated probability level) comparing the $_\Delta V$ among species, site and the interaction of species and sites as a function of distance (data transformed by arcsine square root). * = $p < .05$, ** = $p < .01$, *** = $p < .001$

Distance	Category		
	Species	Site	Species × Site
1 m	45.3 ***	2.8	15.5 ***
5 m	106.1 ***	0.3	28.7 ***
10 m	20.9 ***	21.5 ***	7.4 **
20 m	34.0 ***	4.4 *	0.3
50 m	11.1 **	76.2 **	24.2 ***
80 m	17.8 ***	27.7 ***	10.9 **

This analysis supports the intuition derived from Fig. 2 that *B. valliceps* calls degraded at a greater rate than *B. woodhousii* calls.

Although the comparison of slopes suggests that site has either no significant effect (*B. woodhousii*) or a marginally significant effect (*B. valliceps*) on overall rates of temporal degradation, the data in Fig. 2 suggest an effect at farther distances but not at closer ones. We performed a series of multivariate analyses of variance to ascertain the differences among species and sites at each distance that $_\Delta V$ was measured. As suggested by the comparison of the slopes of the regressions, there was a significant difference in the $_\Delta V$ among the two species at all distances (Table 2). Differences among sites were apparent only at the farther distances (Table 2). There was also a significant species by site interaction at all but one distance, suggesting that the environment affected the calls of the two species differently. It is not known if these environmental factors were consistently different among sites, or were due to differences in atmospheric conditions among days.

Discussion

Unlike attenuation in sound pressure, under ideal conditions $_\Delta V$ should not change with distance. However, the temporal structure of the calls of two species of toads degraded progressively over distance transmitted. This change in the ratio of pulse to interpulse amplitudes can be contrasted with the rate of decrease in overall sound pressure; that is, signal attenuation.

Most animals perceive sound through changes in pressure. Decrease in signal amplitude, due to the dissipation of energy through the spherical spreading of sound, predicts the minimum change of signal amplitude as a function of distance. Actual sound pressure decreases linearly with distance from the source. (By actual sound pressure we refer to a direct measure of pressure, such as dynes/cm^2, rather than a logarithmic comparison, such as dB SPL, in which dB SPL = 20 log [pl/pr], where pr is a reference pressure, usually .0002 dynes/cm^2, and pl is the pressure of the signal.) According to this formula, sound pressure decreases by 6 dB with every doubling of distance from the source, because −6 db = 20 log 0.5.

The slopes of the regressions for ΔV as a function of distance are all far less than -1.0. Thus although ΔV decreases with distance, it appears to do so at a rate much lower than overall signal amplitude. This need not suggest that degradation of temporal structure is less important than signal attenuation. This could only be determined if behavioral thresholds for ΔV, signal amplitude, and interaction of these two characters were known.

Temporal degradation was significantly different between the two species tested. Although differences in spectral components can influence rate of temporal degradation, these species appear too similar in the dominant frequencies of the calls for this to have been an important effect. Temporal components, especially pulse-repetition rate, are very different between these species. Initially, it might be expected that the *B. woodhousii* call should be more susceptible to temporal degradation because it is produced at a higher repetition rate (ca. 125 Hz versus 40 Hz); WILEY & RICHARDS 1982). However, this is only true if the calls have similar pulse durations. Perhaps decrease in the ΔV results primarily from temporal smearing, which is caused by the asynchronous arrival of sounds travelling multiple pathways. The longer the pulse the more likely that the time of arrivals from various pathways will overlap the pulse. The *B. valliceps* calls used in our experiments had pulses twice as long as the *B. woodhousii* calls (10.8 versus 5.1 ms). This might explain the differences in rate of change of ΔV between these toads. However, it is not known how much of the decrease in ΔV is due to smearing rather than to the addition of background noise to the interpulse interval. These experiments do not allow any conclusions as to the cause of these species differences.

There were also differences among sites in rate of change in ΔV, differences that were more apparent farther from the source. Site differences are not surprising because the physical structure of the environment influences the amount of reflection and scattering of sound waves. Also, among-day variation in atmospheric conditions could cause the among-site differences since atmospheric turbulence can introduce amplitude fluctuations which also could decrease ΔV. Turbulence should especially influence low rates of AM (< 10—20 Hz; WILEY & RICHARDS 1982). This study was not designed to investigate among-site variance in transmission characteristics. Instead, our sites were selected to typify breeding areas of these two species of toads; thus they are similar in vegetational composition and do not attempt to test the extremes of potential environmental effects on AM degradation. For example, temporal degradation should be greater in forests than in the open field where we conducted our experiments. The enhanced degradation present at farther sites is expected in any habitat because the number of multiple pathways for sound to travel from source to receiver increases as a function of distance.

The magnitude of temporal degradation revealed in this study could have biological importance for call recognition by female toads. ROSE & CAPRANICA (1984) showed that in two species of toad, *B. americanus* and *B. fowleri*, there were AM tuned units in the torus semicircularis, and that the median of the distribution of AM rates tended to be lower for *B. americanus*, which had the lower pulse repetition rate, than for *B. fowleri*, which had a higher pulse repetition rate. Although the AM "tuning" was defined as the rate of AM that elicited a response with the lowest ΔV, ROSE & CAPRANICA only presented actual data on threshold depth of AM (analogous to ΔV) for three units; these values ranged from 0.35—0.65. At the source, the calls of *B. valliceps* and *B. woodhousii* have a ΔV of about 0.95; if they possess units similar to those subjects studied by ROSE & CAPRANICA, these calls would be suprathreshold not only for units tuned to the respective rates of AM of the call, but also to units with a range of ca. +/− 10 Hz. At a distance of 80 m, ΔV had decreased to 0.143—0.584. Extrapolation from the neurophysiological data suggests that the AM degradation we measured over this distance could result in signals being subthreshold for some temporally tuned units in the torus. At these distances species-recognition information encoded in rate of AM might not be able to be decoded by the auditory system due to decreased ΔV.

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