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SOUND DEGRADATION AND DISTANCE ASSESSMENT BY SONGBIRDS

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INTRODUCTION

Bird song has provoked interest and experiment for a considerable length of time (Lucretious writing in ~70BC (1) and Barrington 1773 (2), respectively), however, the acoustics of song transmission did not receive attention until relatively recently (eg. 3). Much of the early interest in this area concentrated on the effect of transmission characteristics of different habitats on features of the songs of the resident species (eg. 4,5). This paper is concerned with the effect of transmission acoustics on the use of song during territorial defence, specifically, the use of acoustic cues to estimate the distance of a rival singing male.

When recorded song is played back to a territorial male, it is commonly found that the strength of response depends on the position of the loudspeaker in relation to the territory boundary.

Birds generally respond more strongly to song playback at the centre of the territory than at the edge (6). The usual interpretation of such results is that although the responding birds hear both types of playback, they respond weakly to the boundary playback because it simulates a singing male outside the territory which poses little threat. If this interpretation is correct, which acoustic cues are used to perform the discrimination?

During transmission through the habitat, song is attenuated (amplitude decreases with distance from the source, mainly because of spherical spreading and absorption) and song is also degraded (distorted by reverberation, differential frequency attenuation and irregular fluctuations in amplitude). Therefore, distant song will tend to be quiet and distorted. Birds should pay more attention to degradation because it provides more reliable cues for distance estimation than attenuation for two reasons. Amplitude is under the control of the singer to some extent, for example a songbird can change the amplitude apparent to a listener by changing the direction in which it is facing. Also the relationship between amplitude and distance changes unpredictably over relatively short time periods (7,8).

The results of playback to Carolina Wrens (Thryothorus ludovicianus) showed that degradation cues can be used to estimate the distance of a singing conspecific when amplitude and position of the speaker in the territory are held constant (9). The experiment found that response to degraded song was the same as to a conspecific singing outside of the territory (song and no approach), whereas undegraded song elicited silent approach, as did singing conspecific inside the territory.

The object of the experiments reported below was to test the generality of this result by looking for an effect of degradation on response strength in two species in very different habitats; great tits (Parus major) in parkland and Western meadowlarks (Sturnella neglecta) in prairie.

If birds discriminate between degraded and undegraded song, this raises the question of the mechanism of degradation assessment. Morton (10) has suggested that birds judge degradation of a song by comparing the stimulus with an undegraded "standard" consisting of a song that the birds sing. The

experiments with great tits and meadowlarks were designed to test Morton's hypothesis by playing each bird two different songs; a song which the test male and/or its neighbours sang (therefore a standard should exist) and a song which it was unlikely to have heard before (no standard).
The adaptive significance of an ability to estimate distance and implications for song learning and song use in territory defence will be discussed.

METHODS

The experiments were done with 32 male great tits in central Oxford (28th March to 29th April 1983) and with 17 male Western meadowlarks in the Assiniboine River diversion, Portage la Prairie, Manitoba, Canada (20th June to 15th July 1983). Most males were colour-ringed and all could be reliably identified by the composition of song repertoires. The territories of experimental subjects and neighbours were plotted and song repertoires recorded before the experiment began.
Each bird was tested with two songs chosen from the repertoires of males out of earshot (<6km >500m for great tits, <12km >1.5km for meadowlarks). One song (the "familiar" song) was chosen because it could be classified as the same song type as a song in the repertoire of the test bird and/or its neighbours. The other song was chosen because it was a different song type from any in the repertoire of the test bird and was not in the repertoire of any male within 500m of the test male - this was termed the "unfamiliar" song. (For a description of song types in the great tit see (11) and for meadowlarks see (12).)
Both familar and unfamiliar songs were played to the test birds in "undegraded" and "degraded" form. These two stimuli were produced by re-recording the same original song after transmission through typical habitat. Undegraded songs were re-recorded from 5m (great tits) or 3m (meadowlarks), degraded songs from 100m (great tits) or 200m (meadowlarks).
To standardize the volume of playback, the sound pressure levels (SPLs) of all songs were measured with a Bruel and Kjaer 2219 sound level meter (slow response, A weighting) under standard conditions and the output settings on the amplifier were adjusted to give peak and average SPL readings that were as similar as possible for the undegraded and degraded songs comprising each stimulus pair.
Each bird was played four stimuli from the same position, well inside the territory boundary (~25m for great tits, ~150m for meadowlarks). Two observers recorded eight measures of response strength: Total Time Responding (TTR) (a bird was taken to be responding if it was singing, calling or within 20m of the loudspeaker, TTR = total time that one or more of these criteria were fulfilled); Latency (LAT) (= time to first song, call or approach); Closest Approach (MINDIST); Seconds of Song (SECSONG) (great tits only); Latency to Song (LATSONG); Number of Song Bursts (BURSTS)(great tits) or Number of Songs (SONGS)-(meadowlarks); Latency to Closest Approach (LATCLOSE); and Seconds within 20m (SECLOSE) (Great tits) or Time within 100m (T<100) and Time within 50m (T<50m) (meadowlarks). (For further details of experimental design and equipment used, see (13,14,15).)

RESULTS

If undegraded song simulates a singing intruding male inside the territory and such a male is a greater threat than one on, or outside of, the territory boundary, we would predict a stronger response to undegraded than to degraded song. This prediction is supported for familiar songs (Table 1). There is a significantly stronger response to undegraded song for all 8 measures of

response for great tits. Meadowlarks show the same effect although fewer measures are significant (3 out of 8 measures (3/8)). The predicition is not supported for unfamiliar songs. In great tits, only one measure shows a significant difference between degraded and undegraded songs and this is in the opposite direction to that predicted. Similarly, in meadowlarks two measures show a significant difference, one in the predicted direction and one in the opposite direction.

2-way analyses of variance for the two species (with birds as blocks, unfamiliar/familiar as the row treatment and degraded/undegraded as the column treatment) confirm that both degradation of, and familiarity with, the stimulus affect response strength. For both species there is a significant interaction component (familiarity x degradation) for 7/8 measures, and in all but one instance the interaction F value is bigger than either of the main treatment effects.

Table I and the analyses of variance show that response is stronger to undegraded than to degraded song only if the song is familiar. The results from both species show that both degradation and familiarity effect the strength of response to playback.

DISCUSSION

The results show that territorial male great tits and Western meadowlarks show a significantly stronger response to undegraded than to degraded song if the song is familiar. Does this mean that males are using cues from song degradation to assess the distance of another singing male as proposed by Richards (9)? It could be argued that degraded song elicits a weak response because it is a less effective stimulus, perhaps because it lacks some species-specific releasing stimuli through degradation. This explanation is very unlikely since the difference in response strength only occurs if the song is familiar. It could be argued that familiar and unfamiliar songs differ in their propensity to loose species-specific releasers as a result of degradation. As the same song was used as a familiar song for one male and as an unfamiliar song for a different male in a number of instances we can discount this explanation. It seems reasonable to interpret the difference in response strength as resulting from the use of degradation cues to estimate the distance of another singing male.

The finding that birds respond differently to degraded and undegraded song only if they sing the song is support for Morton's (10) proposed mechanism for degradation assessment (comparison with an undegraded internal standard in this case, the song the bird sings).

It is known that two components of sound degradation are important for auditory distance perception in humans (reverberation (16,17), frequency spectrum changes (18)). There is also a suggestion that familiarity with the stimulus affects distance perception (19). An experiment analogous to those done on great tits and meadowlarks has confirmed that degradation and stimulus familiarity are important in relative auditory distance estimation in humans (20). Thus, an effect of degradation and familiarity on distance estimation may be a general phenomenon.

The selective advantage of an ability to use acoustic cues to decide whether a conspecific is inside the shared boundary is that it will reduce the time and energy expended in interacting with neighbouring singing males when they do not pose a threat to the territory. Krebs et al. (21) and Falls et al. (22) following Morton (10), have gone further and suggested that "distance signal-

ling" between neighbouring males may be possible if birds estimate distance using degradation cues and if birds match songs (a common pattern of song use during territory defence in which male replies with the song type that a second is singing). The idea is that when a bird matches a rival it announces that it can judge the rival's distance (ie. it has an appropriate undegraded standard) and also tells the rival about the distance between the two birds (since it is singing a song for which the rival also has a standard).

This hypothesis and the more general advantage of distance estimation may have consequences for the pattern of song learning. Many species learn songs from territorial neighbours (rather than fathers), it could be argued that this pattern results from the advantage of possessing appropriate internal standards in order to assess degradation.

Therefore, a feature of song transmission imposed by the acoustics of the habitat could have important consequences for such diverse areas of song research such as song learning and the way song is used in territory defence - song matching. It also focusses attention on songbirds as adapted listeners (signal receivers) as well as considering them from the more usual angle of signallers.

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SOUND DEGRADATION AND DISTANCE ASSESSMENT BY SONGBIRDS

Table 1

Responses of birds to playback of undegraded and degraded songs that were familiar (FAM) or unfamiliar (UNFAM). Values are $\bar{x} \pm 1SE$. The p value is 2-tailed for Wilcoxon matched-pairs signed-ranks test between responses to undegraded and degraded songs within FAM and UNFAM categories.

MEASURE*		UNDEGRADED	DEGRADED	p
a) Great tits (n=32).				
TTR	: FAM	271.3 ± 19.0	153.9 ± 17.8	<<0.001
	UNFAM	199.2 ± 20.2	217.3 ± 21.8	0.242
LAT	: FAM	29.9 ± 5.9	92.8 ± 22.1	0.005
	UNFAM	75.3 ± 15.1	88.4 ± 20.8	0.768
LATSONG	: FAM	48.9 ± 13.4	118.6 ± 25.5	0.004
	UNFAM	103.7 ± 22.3	105.5 ± 22.3	0.844
LATCLOSE	: FAM	89.4 ± 11.3	173.4 ± 20.4	0.01
	UNFAM	151.1 ± 16.6	165.1 ± 20.9	0.55
MINDIST[1]	: FAM	15.9 ± 3.2	25.4 ± 4.1	0.039
	UNFAM	25.7 ± 4.8	21.0 ± 4.84	0.582
BURSTS[2]	: FAM	24.1 ± 2.5	14.8 ± 1.9	0.009
	UNFAM	22.8 ± 2.4	20.1 ± 2.5	0.624
SECLOSE	: FAM	165.9 ± 27.1	79.2 ± 17.7	0.042
	UNFAM	96.5 ± 19.8	150.5 ± 24.5	0.007
SECSONG	: FAM	162.8 ± 16.9	101.8 ± 13.7	0.0075
	UNFAM	157.5 ± 17.3	132.0 ± 17.3	0.624
b) Western meadowlarks (n=17).				
TTR	: FAM	448.9 ± 7.7	342.9 ± 34.5	0.002
	UNFAM	396.4 ± 47.3	367.2 ± 40.0	0.779
LAT	: FAM	23.3 ± 5.0	101.5 ± 30.8	0.007
	UNFAM	82.2 ± 30.6	56.4 ± 30.8	0.048
LATSONG	: FAM	95.0 ± 38.6	165.0 ± 40.7	0.055
	UNFAM	150.0 ± 45.0	131.1 ± 47.1	0.065
LATCLOSE	: FAM	117.1 ± 25.8	159.0 ± 35.6	0.33
	UNFAM	146.2 ± 31.4	174.3 ± 37.9	0.795
MINDIST[1]	: FAM	53.7 ± 13.5	75.6 ± 15.8	0.35
	UNFAM	46.7 ± 12.2	98.2 ± 22.7	0.033
SONGS[2]	: FAM	17.7 ± 3.2	11.3 ± 2.8	0.072
	UNFAM	15.1 ± 3.0	14.9 ± 2.8	~1.0
T<100	: FAM	365.9 ± 41.0	260.0 ± 51.9	0.022
	UNFAM	281.3 ± 53.0	202.1 ± 55.4	0.131
T<50	: FAM	187.2 ± 49.0	91.8 ± 40.9	0.061
	UNFAM	184.5 ± 47.3	114.7 ± 46.8	0.076

*All values are secs., except: 1 = metres; 2 = number.
See Methods for explanation of response measures.

SOUND DEGRADATION AND DISTANCE ASSESSMENT BY SONGBIRDS

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