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GENERAL BIOLOGY

Situational Changes in Vocalization of Great Gerbils *(Rhombomys opimus Licht)* During Defensive Behavior

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The relevance of animal acoustic signals in a particular situation is a complicated problem in bioacoustics [5]. Different sounds are emitted in different situations, and the changes in vocalization can reflect the changes occurring in the animal's arousal or emotional state. These signs are very important in communication between partners or rivals [3]. The situation-relevant changes in vocal behavior are poorly understood; however, some principles seem to be established [1,7,9, 11], which may be shared by most mammals [10]. Investigating the situation-relevant vocalization is a complicated task not only because of the complexity of analyzing audio and video recordings, but also because of the difficulties in placing an appropriate model object in a desired situation. In this respect, the great gerbil is an appropriate object. Confronting a gerbil with a conspecific on a neutral territory (a small chamber) often causes conflicts, usually stereotyped and accompanied with vocalizations from the defending animal. These uniformly structured calls are closely related to a full set of easily discernible expressive movements, which are performed at a slower pace than in other gerbil species. The situations, in which the calls are emitted, are easily reproducible in a number of trials. This report summarizes the results of a preliminary study designed to reveal a quantitative relationship between changes in the acoustic parameters of calls emitted by the defending animal and the situational tension, as estimated by the distance between the animals and the direction of attention of the defending animal.

Great gerbils were kept in the vivarium of the Department of Zoology of Vertebrates at Moscow State University. The animals were caged by pairs or triples for one month prior to tests. The animals that had never met before or were separated for at least one month were confronted.

The gerbils were put in pairs into a chamber made of a cloth-based plastic (60 x 77 x 60 cm) with a transparent forewall. The floor of the chamber was divided into 10 x 10 cm squares. The chamber was illuminated with two 40 W luminescent lamps placed 70 cm above the floor. Each pair was kept in the chamber for 20 min; a total of 45 tests were performed with 24 gerbils (7 males and 17 females) aged 2 months to 2 years. Each animal was tested in 1 - 9 trials, but never more than once a day. Further analysis was based on 17 videotaped trials with 4 males and 8 females selected for clearly expressed aggressive behavior and multiple sound calls.

The gerbil behavior was videotaped using two LOMO-VK-1/2 video recorders, one of which filmed the general view from beneath the chamber, while the other was recording the frontal plane. Acoustic signals were recorded on a Rostov 102 stereo tape recorder (at 9.5 cm/s tape speed) using a LOMO-82A moving-coil microphone.

The frequency-time characteristics of the acoustic signals were analyzed on a Spectr-1 dynamic spectrograph equipped with 46 parallel filters (0.2 to 16 kHz). A total of 139 sounds recorded in 9 trials were analyzed on a Kay Electric 7026 sonograph.

In addition to the recordings made in this work, our description of gerbil vocal behavior is based on 197 previously recorded tapes and sonograms [1]. However, in contrast to the previous study, the long signals (types 7 and 8 according to our classification) were fragmented so that they could be analyzed as syllables.

In order to evaluate the situation-dependent variability of sounds in the 17 selected trials, we analyzed every fifth minute in the sonogram. The gerbil behavior was evaluated using two parameters: (1) the distance, which was considered long or short depending on whether it exceeded the length of the animal's body; and (2) the direction of attention of the vocalizing animal dichotomized according to whether or not it was concentrating on the partner's movements. The animal was considered concentrating if it, appreciably for the observer, reacted upon or apparently gazed at the rival's movements. The animal was considered not concentrating on its partner if it did not react on the partner's movement, but instead displayed foraging or self-grooming behavior; explored feces, urine spots, or the chamber; or jumped on the walls of the chamber.

To avoid any effect of vocalization of the expert evaluation of behavioral variables, this analysis was performed on tapes played mute.

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Table 1. Types of vocalization emitted by great gerbils in defensive behavior

Call type	N*	n*	Base frequency, kHz ($M \pm SE$)				Duration, ms ($M \pm SE$)		
			maximum	initial	final	depth of frequency modulation	total	leading edge	trailing edge
1	17	75	3.61 ± 0.09	1.96 ± 0.04	1.81 ± 0.05	1.89 ± 0.09	261.6 ± 10.4	53.8 ± 2.2	96.3 ± 6.1
2	21	82	3.36 ± 0.07	1.89 ± 0.04	1.75 ± 0.04	1.69 ± 0.06	170.0 ± 7.3	62.7 ± 3.4	70.2 ± 4.8
3	19	85	2.57 ± 0.04	1.83 ± 0.04	1.65 ± 0.05	0.95 ± 0.04	99.0 ± 5.2	39.8 ± 2.5	39.1 ± 2.7
4	12	62	1.96 ± 0.06	1.51 ± 0.05	1.52 ± 0.04	0.57 ± 0.04	174.5 ± 12.8	58.4 ± 6.3	53.3 ± 5.5
5	11	32	1.59 ± 0.05	1.55 ± 0.05	1.52 ± 0.05	0.09 ± 0.02	118.6 ± 17.1	11.6 ± 3.0	15.5 ± 3.2

* N is the number of animals; n is the number of calls.

The changes in the acoustic signals were analyzed by comparing calls emitted in different situations. The situational parameters registered were the long or short distance between partners, whether or not they were concentrating on each other, and all pairwise combinations of these variants: whether or not the vocalizing animal concentrates on its partner being separated by a short or long distance.

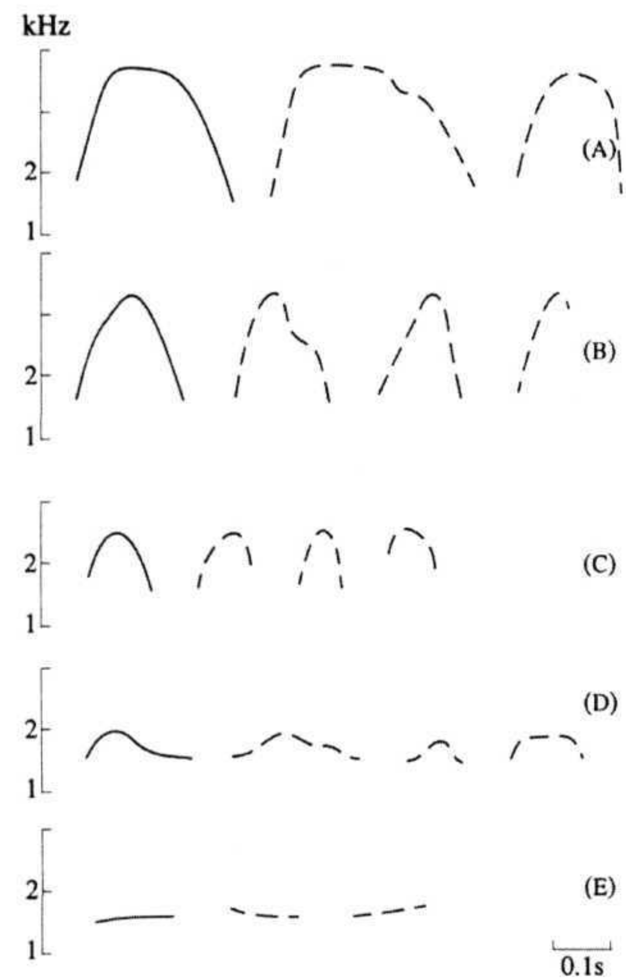

Fig. 1. Changes in base frequencies of different type calls emitted by great gerbils in defensive behavior. A, type 1; B, type 2, C, type 3; D, type 4; E, type 5. Dotted lines show possible patterns of frequency modulation within the type.

The acoustic parameters analyzed were the length, maximal frequency, depth of frequency modulation (the difference between maximal and minimal frequencies), and monotony (the ratio of the signal length to the depth of frequency modulation).

In every analysis we calculated: (1) the relative length of vocalization (the ratio between the total duration of all signals emitted to the length of a given situation); (2) the rate of signals in the sequence; and (3) the mean interval between calls.

The acoustic parameters of vocalization emitted in various situations were compared using the Wilcoxon matched-pairs test. Percent ratios were compared using the White test of ratios [2].

An analysis of 336 calls allowed us to divide them into 5 types.

Type 1 is characterized by a rapid increase in the base frequency to its upper limit in the beginning of the sound. The frequency is subsequently kept at that level (sonographic plateau) with slight frequency modulation, followed by an abrupt drop in frequency by the end of the sound. The sonogram is nearly square-shaped (Table 1 and curve A in the figure).

Type 2 is characterized by a slow rise and fall in the base frequency, which nearly reaches the values of the type 1 calls. The base frequency could reach its maximum in the beginning or the end of the signal, but mostly in its midpoint. The shape of the sonogram is nearly triangular (Table 1 and curve B in the figure).

Type 3 is a short call similar to type 2 calls in its frequency modulation pattern, but having a lower maximum base frequency (Table 1 and curve C in the figure).

Type 4 is a long call featuring a complex pattern of frequency modulation with alternating modulated and nonmodulated fragments and a variable shape of frequency modulation (Table 1 and curve D in the figure).

Type 5. Narrow-band nonmodulated or weakly modulated monotonous low-frequency calls. The sonograms display horizontal lines of widely varied lengths (Table 1 and curve E in the figure).

Table 2. Characterization of calls emitted in various situations

Parameter	Pairs of situations compared				
	w *vs* nw	s *vs* l	ws *vs* sl	wl *vs* nwl	ws *vs* nwl
Duration	>	>	>	>	>
Maximal Frequency	>	>	>	>	>
Depth of frequency modulation	>	>	>	>	>
Monotony	<	<	<	<	<
Relative total duration of vocalization	>	>	>	>	>
Sound pulse rate	>	>	ns	>	>

Note: In each pair, the situation specified on the left is more tense and that specified on the right is less tense. The sign of the inequality indicates whether the parameter is greater or lower ($p < 0.01$ by Wilcoxon test) in the first of two situations than in the second. w is concentrating attention on the partner, nw, not concentrating; s, short distance; l, long distance; ns, not significant.

The characteristics of acoustic signals recorded in different situations are presented in Table 2.

In evaluating the ferocity of antagonism in each situation, we presumed that the shorter the distance, the more tense the situation was, provided that all other conditions were similar. A situation with an animal's attention concentrated on its partner was considered more tense than that with no concentration. All further conclusions were made assuming the *a priori* correctness of these basic postulates.

A range of acoustic parameters correlated with changes in the situational tension. In each pair, the more tense situations involved more frequent and longer sounds at shorter intervals, with a higher maximal frequency and greater depth of frequency modulation.

A comparison of the incidence of sounds in situations of varied tension showed that all sounds could be divided into two groups. Types 1 and 2 prevailed in more tense situations and were more frequent in the more tense situations compared. The second group of sounds was composed of types 3 to 5 prevalent in less tense situations. In our previous work [1], we noted that menacing abrupt movements of the rival caused frequency-modulated sounds from the defending gerbil, whereas low-modulated sounds of the defending animal were characteristic of the absence of rapid movements on the part of the aggressor. The latter vocalization is similar in structure to that emitted by gerbils in a "peaceful" situation, when the partner remains unresponsive to repeated submission attempts for grooming. This suggested that the rapid increase in the tone frequency reflects the motivation of fear, whereas monotonous sounds may reflect frustration. There is no definite evidence that the change between these motivations reflect the transition from one of the compared situations to the other. There are at least two intrinsic determinants of the structure of sounds emitted in a given situation. These factors can be termed "fear", which dominates in more tense situations and causes type 1 and 2 sounds, and "frustration", which is characteristic of less tense situations and related to type 4 and 5 sounds.

Type 3 sounds occupy a peculiar position on that scale. They are similar in structure to those of the first group. However, they are closer to group 2 in their relationship with situational tension. This is the only type of frequency-modulated sounds occurring more frequently, rather than becoming rare, with the elongation of distance. This deserves special attention because the structure of type 3 sounds is most similar to that of alarm signals of danger (described in [4] in more detail). The base frequency of these signals recorded in our laboratory has a maximum of 3.06 ± 0.05 kHz ($n = 28$) with the pulse length of 91.8 ± 3.9 ms. The main difference between type 3 and alarm signals is that the former are emitted in a rhythmically organized series. The alarm signals of danger are accompanied by a special predator-defensive behavioral complex: alerted postures, paw tapping, retreat into the burrow with a characteristic leap, and throwing sand with hindpaws [1]. This behavioral pattern is ordinarily elicited by the appearance of an alarming object near the burrow; however, it may also be observed in gerbil conflicts with a conspecific (although certain postures and the alerting signal rarely occur). The genesis and functions of alarm signals is one of the most often discussed issues in socioecology [5, 6, 8, 12]. However, the structural

Table 3. Occurrence of call types in different situations

Call type	Pairs of situations compared				
	w *vs* nw	s *vs* 1	ws *vs* sl	wl *vs* nwl	ws *vs* nwl
1	>>	>>	>>	>>	>>
2	>>	>>	ns	>	>>
3	ns	<<	<	ns	<<
4	ns	<<	<<	ns	<
5	<<	<<	ns	<<	<<

Note: The sign of the inequality indicates that the percentage of calls of a given type emitted in the first situation is significantly greater or lower than in the second situation of the pair. >>, - $p < 0.01$; >, - $p < 0.05$. See Table 2 for other designations.

relationship between the species behavioral and acoustic repertoires often remains beyond the scope of discussion. In contrast, much attention is focused on the value of these calls in manipulating the behavior of neighboring individuals in order to ensure the animal's own survival or the survival of its relatives. We believe that the structural similarity of the alerting signal of danger to the signals (featuring a distinct complex of structural and situation-relevant characteristics) of antagonistic behavior may be central to the solution of the nature of the phenomena described here.

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