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Acoustic Activity Displayed in the Agonistic Behavior of Great and Light Gerbils

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The solution of many topical problems of modern biology, in particular, behavioral ones, is based on the comparative approach, i.e., detection of differences between species or populations. This stimulated the search for new methods of comparative description of behavior. At present, methods describing behavior as a continuous dynamic process [1, 3, 11-13] are being developed, which are alternative to a separate description of single species-specific stereotypic positions and displays interspersed in a behavioral continuum. However, all these studies are aimed at analysis of the dynamics of motor behavior, whereas the possibility of using dynamic characteristics of acoustic behavior in a comparison between species has not yet been investigated.

The aim of this study was the investigation of differences in the acoustic activity accompanying the experimentally induced agonistic behavior in two gerbil species. This work was based on the analysis of acoustic activity of the loser, which was studied in connection with the intensity of agonistic behavior and the distance between partners. The objects of study were two gerbil species that are different in their social ecology: great gerbils *Rhombomys opimus*, which are characterized by family- and team-associated habits, and light gerbils *Gerbillus perpallidus* characterized by solitary habits [6, 8, 9]. In these two species, acoustic signals accompanying defensive behavior fall within the auditory band and can easily be recorded and analyzed [4, 7].

In our experiments, we used male gerbils maintained at the vivarium of the Department of Vertebrate Zoology and General Ecology, Moscow State University (15 and 20 great and light gerbils, respectively). All males were sexually mature and were older than 8 and 3 months (great and light gerbils, respectively). Males were maintained in pairs with females or singly in plastic cages, which were covered with a netted top and had a size of 45 x 30 x 20 cm. Wood sawdust served as ground litter. Gerbils were fed oat and sunflower grains, dried bread, and carrot and apple slices. The food was available in plenty; animals did not receive water. A photoperiod typical of Moscow and a temperature of 18 to 23°C was maintained in the experimental compartment.

In our experiments, we placed gerbils, which were individually marked with ursol black D, in pairs into a neutral territory, a textolith chamber (76.5 x 58 x 65 cm), in which the front wall was glazed. There was no ground litter in the chamber. Prior to each experiment, the chamber was rinsed with water and cleaned with ethanol to eliminate odors. The experiments were conducted after midday in the beginning of the reproductive season, from March to June.

In these experiments, we used only gerbils that were not genetically related or familiar with each other. Each male participated in experiments no more than once a day and no more than six times per complete experimental session. Using clean glass cans, we took gerbils from cages, and partners were simultaneously let out of cans onto the floor of the chamber. For great and light gerbils, the duration of experiments was 30 and 15 min. respectively. The experiment was recorded by two synchronized video cameras, one recording from above and the other taking a side view.

For statistical treatment, we selected the experiments with great and light gerbils (20 and 15 tests, respectively) in which a stable asymmetry was established between partners; i.e., one of the opponents (winner) continued threatening and attacking, whereas the other (loser) only defended, put itself into submissive positions, and escaped [5]. When threatening a loser, winners never cried but occasionally chattered with teeth, whereas the motor activity of the loser was often accompanied by sounds from the defensive repertoire.

In the treatment of video records with the help of the method of scan sampling [10] (a sample every second), we registered the distance between partners (measured in body lengths) and the form of the winner's behavior. Using the "one-zero" method [10], we detected the

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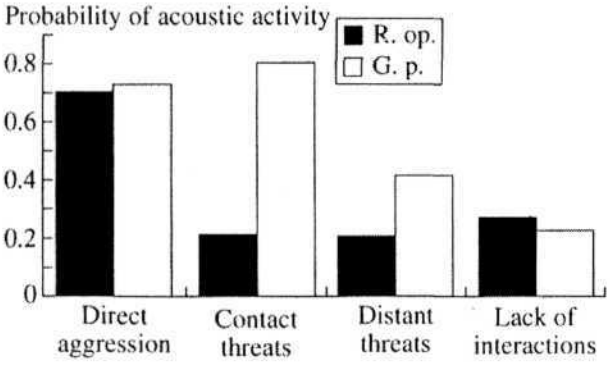

Fig. 1. The probability of acoustic activity of loser in relation to the form of interactions in (R. op.) great and (G. p.) light gerbils.

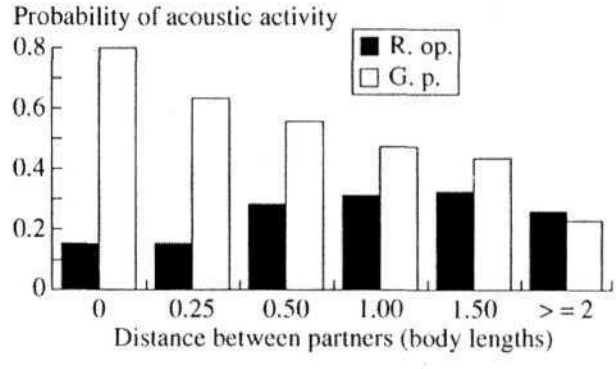

Fig. 2. The probability of acoustic activity of loser in relation to the distance between partners in (R. op.) great and (G. p.) light gerbils.

presence or absence of the loser's cries during each second.

After establishing the asymmetry between partners, winners displayed only the aggressive (during interactions) and exploratory (during the intervals between interactions) forms of behavior (the forms were separately described in [7]). The aggressive forms of the winner's behavior were divided into three groups in accordance with the intensity of interactions between partners: low-intensity interactions including various forms of distant threats, medium-intensity interactions including a variety of contact threats, and high-intensity interactions comprising the elements of direct aggression (attack, fight, and pursuit).

The probability of the loser's acoustic activity was calculated as the ratio between the number of 1-s scan samples during which the loser displayed acoustic activity and the total number of 1 -s scan samples during which a given distance was maintained or a given form of the winner's behavior was observed.

In total, 34022 and 15308 1-s scan samples were analyzed for great and light gerbils, respectively. The data were statistically treated using the software package STATISTICA, version 4.5. To test the significance of differences in the probabilities given in pairs, we used White's test for comparison of fractions.

After establishing the asymmetry between partners, the probability of the acoustic activity of the loser was significantly greater in light gerbils than in great ones. Light gerbils cried during 39.3% of experimental time, whereas great gerbils, during only 22.8% ($p < 0.001$).

This was related to the fact that great gerbils cried significantly more rarely ($p < 0.001$) in the threatening demonstrations (Fig. 1). Only directly aggressive activities were highly probable to be accompanied by the loser's cries in great gerbils. This was the situation in which no significant differences were found between great and light gerbils. As all contact threats and an overwhelming majority of distant threats occurred in the cases when the distance between partners was no more than 1.5 body lengths, the acoustic activity displayed at these distances was also significantly lower in great gerbils than in light ones ($p < 0.001$ in all cases; Fig. 2). However, the probability of acoustic activity displayed at larger distances (no less than two body lengths) or in the absence of interaction between partners was significantly higher in great gerbils than in light ones ($p < 0.001$ in both cases). Moreover, in great gerbils, the probability of acoustic activity of the loser was significantly higher both in the absence of aggressive interactions and at a distance of no less than two body lengths between partners than in the case of distant and contact threats and at a distance of 0 to 0.25 body lengths, respectively ($p < 0.001$ in all cases).

Thus, we found significant interspecies differences in the pattern of acoustic activity observed during agonistic interactions between great and light gerbils. When interactions occur at short distances and have a higher intensity, the probability of acoustic activity of the loser is significantly higher in light gerbils than in great ones. Conversely, when interactions are nonaggressive and occur at a distance of more than 1.5 body lengths, the probability of acoustic activity of the loser is higher in great gerbils than in light ones. Moreover, these species differed with respect to the direction of change in the probability of acoustic activity. In light gerbils, the probability of acoustic activity of the loser linearly grew with a decrease in the distance between partners and with an increase in the intensity of interactions. By contrast, an uneven decrease in the probability of acoustic activity of the loser occurs in these situations in great gerbils.

Why are great gerbils characterized by a higher probability of acoustic activity at short distances between partners in the absence of interactions than in the case of approaching partners during threats? It is known that the cries of loser gerbils are often coincident with the motor activities of the winner or the loser itself [7]. Therefore, the observed interspecies differences in the acoustic activity may reflect both species-specific features of locomotion of gerbils, which were

displayed during aggressive opposition, and their reaction to motion.

Earlier, we demonstrated that, in great gerbils, a change in the distance between partners occurs more rarely during aggressive interactions than between interactions. Conversely, light gerbils more frequently change the distance during interactions than in the absence of interaction [2]. Thus, in light gerbils, the motion activities of partners relative to each other, which provoke cries, are more frequent during interactions; in great gerbils, they are more frequent during the intervals between interactions.

Moreover, during aggressive interaction, great gerbils spend up to 80% of time in prolonged oppositions, when both the distance between partners and the configuration of bodies remain invariable. Conversely, interacting light gerbils change the distance every other second of interaction. During the seconds when the distance does not vary, the partners synchronously move relative to each other in 50% of cases [2]. Thus, the interspecies differences in the dynamics of acoustic behavior can indeed reflect species-specific features of the rhythm of interactions in great and light gerbils.

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