Rodent Ultrasonic Short Calls: Locomotion, Biomechanics, and Communication

Mark S. Blumberg
Indiana University

Rodents of many species emit short ultrasonic vocalizations during copulation, aggression, and other activities. Thiessen and Kittrell (1979) hypothesized that ultrasound emission by gerbils is the acoustic by-product of physical compression of the thorax during certain locomotor behaviors. I carry this hypothesis further by relating gerbil ultrasound to the biomechanics of respiration during locomotion. I also suggest that at least some of the ultrasonic emissions of other rodent species are, like the gerbil's, by-products of thoracic compression during locomotion. Support for this suggestion comes from descriptions in the literature of ultrasound emission as well as slow-motion analysis of rat copulatory behavior. Finally, this alternative view of rodent ultrasound has consequences for the interpretation of experimental findings in ultrasound research and for the understanding of messages and meanings in rodent communication.

Rats and other rodents emit high-frequency (ultrasonic) vocalizations in various contexts over the course of the life span (Noirot, 1972; Nyby & Whitney, 1978). These vocalizations can be divided roughly into three classes based on the age of the vocalizing animal, the context in which the vocalization is produced, and the characteristics of the vocalization. First, rodent pups emit ultrasonic *distress* vocalizations when exposed to cold (Allin & Banks, 1971; Okon, 1971). Second, adult male rats emit a 22-kHz vocalization after ejaculation (Barfield & Geyer, 1972), after defeat in an aggressive encounter (Sales, 1972a), and during the induction of fever (Blumberg & Moltz, 1987). Recently, it was hypothesized that both of these vocalizations are acoustic by-products of a respiratory mechanism (i.e., laryngeal braking) that enhances gas exchange in the lungs (Blumberg & Alberts, 1990, 1991).

This article concerns a third class of rodent ultrasound. These vocalizations are short pulses produced by rodents of many different species during mating, aggressive encounters, and other contexts that involve high levels of behavioral arousal. For example, ultrasonic vocalizations that accompany copulation have been detected from male and female collared lemmings (*Dicrostonyx groenlandicus*; Brooks & Banks, 1973), male and female rats (*Rattus norvegicus*; Thomas & Barfield, 1985), and male mice (*Mus musculus*; Sales, 1972b), as well as from members of other species (Sales, 1972b). Similarly, calls that accompany aggressive encounters have been detected from the males of many rodent species including rats, mice, hamsters (*Mesocricetus auratus*), and voles (*Microtus agrestis*; Sales, 1972a). In addition, not all rodent vocalizations are ultrasonic; for example, male woodrats (*Neotoma lepida*) emit an audible rasping vocalization during copulation (White & Fleming, 1987).

The observed emission of these vocalizations during copulation led naturally to the hypothesis that the calls facilitate sexual behavior. Experiments have borne out these hypotheses to some extent, although different species exhibit different responses. For example, when recordings of a male hamster's copulatory vocalizations are played to an estrous female, the lordosis posture of the female is prolonged (Floody & Pfaff, 1977c); in other words, vocalizations appear to enhance receptivity in female hamsters. In contrast, male rat copulatory vocalizations result in increased female solicitation behaviors, such as darting and hopping (Thomas, Howard, & Barfield, 1982); in other words, vocalizations appear to enhance proceptivity in female rats. The short calls that accompany aggressive encounters have been suggested to be a means of inducing the submission of another animal without resorting to overt conflict (Sales, 1972a), although this has not yet been demonstrated (see Graham & Thiessen, 1980). Therefore, in at least some rodent species and especially during sexual behavior, these vocalizations appear to affect the behavior of conspecifics in ways that seem to benefit the vocalizing animal.

Biomechanical Basis of Gerbil Ultrasound

As described, conspecific behavior can be modified by these short ultrasonic pulses. However, Thiessen and his colleagues (Thiessen & Kittrell, 1979; Thiessen, Kittrell, & Graham, 1980), studying Mongolian gerbils (*Meriones unguiculatus*), were unable to identify a communicatory effect of ultrasound. They decided, therefore, to investigate the characteristics of ultrasound emission by gerbils. They reasoned that if they knew how and under what circumstances the vocalization is emitted, they could get a better idea of how the vocalization serves a communicatory function.

Thiessen and Kittrell (1979) found a very strong association between the emission of the vocalization and a number of different modes of locomotion.

> The most typical mode, accounting for as much as 90 percent of all ultrasounds, is a hop. Very often, as an animal moves swiftly

across an area, all four feet leave the ground. As the forepaws touch the ground on landing an ultrasound is emitted. (p. 511)

There are other kinds of body movements in which ultrasound is emitted, including turning, stretching, compression of the upper body, and hind foot thumping. All of them share a common feature: "The common denominator of these modes of ultrasonic production is a physical compression of the lungs and the forcing of air through the larynx and out the nose" (Thiessen & Kittrell, 1979, p. 511).

On the basis of their findings, Thiessen and Kittrell (1979) suggested that gerbil ultrasounds may be the "artifacts of general behavioral activation, somewhat akin to the wheezing of an exercised horse" (p. 509). This statement is clearly at odds with the conventional wisdom that interprets ultrasound production by rodents as communicatory signals that are emitted in order to serve specific communicatory functions.

In this article, I place gerbil ultrasound into a broader biomechanical context and then use this context to explain how other rodent ultrasonic emissions may be similarly interpreted. I also show how sensitivity to these biomechanical issues leads to alternative interpretations of experimental studies of rodent ultrasound. Finally, the consequences of this view for understanding the communicatory effects of ultrasound emission is discussed.

Breathing Patterns During Locomotion in Mammals and the Role of the Larynx

The analogy of gerbil ultrasound with the wheezing of an exercised horse is very illustrative, but more can be said. Specifically, the fact that gerbils emit ultrasound as the forepaws hit the ground is consistent with current understanding of how mammals breathe during locomotion. Furthermore, the fact that ultrasound production by gerbils is diminished or eliminated by denervation of the laryngeal nerves (Thiessen et al., 1980) is consistent with our current understanding of the activity of the larynx during respiration as well as its possible usefulness during locomotion. These two issues, the timing of breathing during locomotion and the role of the larynx, are dealt with in turn.

Respiration and Locomotion

The study of respiratory patterns during locomotion is rather new (Bramble, 1989; Bramble & Carrier, 1983), and the number of species that have been studied is limited. Many of the main findings, however, appear to be generalizable. For example, in quadrupedal species, breathing and locomotion become coupled so that one breathing cycle passes with each stride, especially at higher running speeds. Such coupling may be the necessary outcome of the facts that both locomotion and respiration require the use of the same parts of the body (i.e., thoracic cage and associated musculature) and that locomotion places great strain on this thoracic complex as the forelimbs make contact with the ground (Bramble & Carrier, 1983). Thus, the breathing cycle is timed so as not to act against the mechanical forces of locomotion.

Bramble (1989) provided a clear discussion of inhalation and exhalation during a horse's gallop. First, inhalation begins

after the horse's forelimbs have left the ground. During this time thoracic and abdominal volume are increased. In addition, the increase in abdominal volume and the forward acceleration of the body result in the rearward displacement of the large visceral organs (especially the liver; referred to by Bramble as the "visceral piston," p. 173). The posterior displacement of the visceral piston and its action on the diaphragm leads to a further increase in thoracic volume.

Exhalation begins shortly after the first forelimb makes ground contact. At this time the thoracic cavity experiences increased loading for a number of reasons. First, reaction forces from the ground lead to a direct compression of the thorax. Second, as the horse decelerates, the visceral piston will begin to move forward into the diaphragm. Third, the forward movement of the animal's pelvis leads to a reduction of abdominal volume and, in turn, a reduction in thoracic volume. All of these actions result in increased intrathoracic and pulmonary pressure. Then, "exhalation begins explosively near the point at which the thoracic complex experiences its peak load" (Bramble & Carrier, 1983, p. 253). This relation between exhalation and forelimb ground contact has been found in every quadruped studied by Bramble and Carrier (viz., jackrabbit, dog, and horse). Sometimes this exhalation can be truly explosive. One dog tested by Bramble often barked when its forelimbs hit the ground (D. M. Bramble, personal communication, January 22, 1990).

Role of the Larynx in Respiration and Locomotion

That gerbils emit ultrasound as their forelimbs hit the ground is consistent with the finding that mammals typically exhale as their forelimbs hit the ground. Furthermore, the fact that intact neural connections to the larynx are necessary for ultrasound production, as is mentioned earlier, suggests that the larynx is constricted during ultrasound emission as the gerbil's forepaws make contact with the ground and as the animal begins to exhale. This suggestion is consistent with observations that the larynx typically dilates during inhalation and constricts during exhalation (Megirian & Sherrey, 1980; Negus, 1929).

Although the activity of the larynx during respiration has received some attention, its activity during locomotion has not. Investigations of laryngeal activity during locomotion are needed because there is reason to believe that laryngeal constriction during forelimb contact and thoracic loading may be beneficial in the following way: With the larynx closed as contact is made, intrathoracic pressure increases, and the thoracic cage becomes fixed. This fixing of the thorax may help the animal to absorb the shock of impact. Interestingly, the larynx of rodents, as well as other mammals capable of independent use of the forelimbs, appears to possess modifications that allow it to withstand high intrathoracic pressures (Negus, 1929; see also Roberts, 1975).

The timing of laryngeal constriction with thoracic loading and exhalation can be accomplished in at least two ways. First, as already stated, laryngeal activity is normally tied to the respiratory cycle. Second, there exists a reflex arc from rib musculature to the larynx, called the *intercostal-to-laryngeal reflex* (Remmers, 1973). With such a reflex, information derived from the stretching of the thoracic cage during loco-

motion may be used to regulate laryngeal dilation and constriction directly.

To sum up, the emission of ultrasound by gerbils can be viewed as the artifact of biomechanical forces that act on the thoracic cage during locomotion. The ultrasound emission is likely reflecting an explosive expiration after forelimb ground contact has been made and the thorax has experienced its maximum load. Laryngeal constriction during thoracic loading may also help the gerbil to absorb the shock of forelimb impact and may complement other structural mechanisms, such as the shock absorption apparatus of the spine (Gambaryan, 1974).

Ultrasound Emission Is Associated With Locomotor Activity and Thoracic Compression in Other Rodent Species

As we have seen, the coincident emission of sound by gerbils during forelimb contact is consistent with the biomechanical basis of locomotion. Next, we need to know the extent to which ultrasound production is related to locomotion and other strenuous behaviors in other rodents. As it turns out, there is considerable evidence that ultrasound production and locomotion are associated across many rodent species studied thus far. Unfortunately, little significance has been attached to this association, perhaps because locomotion does not accompany all ultrasound production (e.g., Dempster, Dempster, & Perrin, 1991; Sales, 1972a).

Sales (1972b) monitored ultrasound production in rats and found that as the male chased the female the emission of ultrasound "appeared to be synchronous with the movements of the male" (p. 105). Similarly, McIntosh and Barfield (1980) found that the 40- to 60-kHz vocalizations of rats occurred in clusters before mounts and intromissions, at which time the female is hopping and darting and the male is chasing and attempting to mount. Thomas and Barfield (1985) found that the female's vocalizations were "sometimes emitted in close temporal proximity to hopping and darting" (p. 721). Similarly, White and Fleming (1987) noted that the audible rasping vocalization of male woodrats "occurs in the period shortly before intromission, coinciding with hop-darting and lordosis in the female, and trailing and mounting in the male" (p. 1281).

Floody and Pfaff (1977a) studied ultrasound production by female hamsters during courting and copulation. They also noted the association between ultrasound production and movement, stating that difficulties in recording the vocalizations "were exacerbated by the tendency of females to call while engaging in abrupt movements of the head and body; for instance, many calls occurred during transitions between short darting runs and the adoption of upright investigatory postures" (Floody & Pfaff, 1977a, 796).

Sales (1972b) described another circumstance that involves ultrasound production and locomotion (see also Sewell, 1968). While she was observing the activities of 22-day-old *Apodemus* young, she noted that ultrasound was detected "as the young ran jerkily round the cage and the calls appeared to be correlated with these movements" (Sales, 1972b, p. 161).

Locomotion is not the only aspect of copulation that places a strain on the upper body. When the male mounts the female during copulation, the male grasps the female's flanks with its forearms and, gripping tightly, performs a series of rapid thrusts. Sales (1972b) found that ultrasounds were emitted while the male rat was intromitting. Furthermore, when she examined other species, such as mice, that have prolonged mount durations, she made an intriguing observation, "the ultrasonic pulses appeared to be correlated with the pelvic thrusts of the male" (Sales, 1972b, p. 152). This phenomenon can be explained in the following way: When the male mounts the female and grasps the female's flanks with its forelimbs, the larynx is likely to be constricted to fix the thorax and thus support the use of the forelimbs in this way (Negus, 1929). Then, as the male thrusts with its hind leg, the abdominal cavity compresses, and in turn, the thoracic cavity compresses. Intrathoracic pressure is then built up, blowing the larynx open and producing a sound.

When the male mounts the female, the female reflexively assumes the lordotic posture. This posture is characterized by arching of the back and dorsoflexion of the tail. Thomas and Barfield (1985) make the following observation: "During lordosis no calls were detected" (p. 721). (Female hamsters also do not call while in the lordotic posture; Floody & Pfaff, 1977a.) Thomas and Barfield continued, "However, the quick reflexive release from the lordotic posture often was accompanied by ultrasonic vocalization" (p. 721). If one assumes that ultrasound emission is related to locomotion in this species, and given that during lordosis the female remains stationary, it is not surprising that no ultrasounds were detected at this time. On the other hand, it may be expected that ultrasound accompanies the "quick reflexive release" out of the lordotic posture because of the forelimb effort and thoracic compression that this movement entails.

As I state earlier, ultrasound emission also accompanies aggressive activities. Sales (1972a) observed such activities in rats and other rodents and recorded both the emission of ultrasound and the behaviors that accompanied it. In some cases ultrasounds accompanied behaviors in which the association with forelimb strain is not obvious (e.g., slow approach and separation after aggression). However, the greatest number of ultrasounds accompanied attack, defined as the rapid approach of one animal toward another. Ultrasounds were also often detected during stand-up boxing (i.e., animals stand on their hind legs facing each other, forepaws to forepaws, and parrying often occurs) and wrestling (i.e., actual fighting, when both animals are locked together and roll around the cage).

Sales (1972b) reported another interesting observation of a lactating female gerbil that was disturbed while out of the nest: "She immediately thumped rhythmically on the ground with one hind foot and pulses at about 50 kHz were detected simultaneously" (p. 161). Recall that Thiessen et al. (1980) also made this observation.

It is clear from these descriptions of various rodents during various behaviors that an association exists between ultrasound emission and thoracic compression. It is not possible, however, to discern from these verbal descriptions the exact nature of this relation. Therefore, as a preliminary investiga-

tion, I observed and videotaped a pair of rats (*Rattus norve-gicus*) during copulation (M. S. Blumberg, unpublished observations, January–February 1990). Recall that Thomas and Barfield (1985) found that female vocalizations were "sometimes emitted in close temporal proximity to hopping and darting" (p. 721). On this basis, I predicted that ultrasounds would be emitted during hopping as the female's forepaws hit the ground or shortly thereafter as the rear of the animal moved forward and compressed the abdomen and thorax.

As I observed the animals during copulation, there was a clear association between movements of the male and female and ultrasound emission, but the exact nature of this association could not be determined until the pair was observed in slow motion. When this was done, it became readily apparent that ultrasound emission often occurred shortly after the female's forepaws touched the ground and the hind limbs began to move forward. In other words, ultrasound emission occurred as the thorax became compressed after a hop. This is exactly what Thiessen and Kittrell (1979) noted in gerbils.

These preliminary observations support the hypothesis that some rodent vocalizations are acoustic by-products of biomechanical strain on the forelimbs and thorax. However, it must be stressed that not all such vocalizations can be so easily related to biomechanical strain; in fact, I observed instances of ultrasound emission that were not clearly associated with strained body movements, as have others (e.g., Dempster et al., 1991). Furthermore, rats that are forced or trained to jump do not emit ultrasound (M. S. Blumberg, unpublished observations, January–February 1990), which suggests that behavioral and physiological arousal are contributing factors. Nonetheless, the association between ultrasound and locomotion is ubiquitous and incontrovertible, which suggests that "physical constraints on ultrasonic production set the range of information that can be conveyed during social interactions" (Thiessen et al., 1980, p. 416).

Consequences for the Interpretation of Past Research

If I am correct in suggesting that many rodent ultrasounds, like those of gerbils, are associated with or are the by-products of biomechanical strain on the thorax and forelimbs, then the interpretation of experiments into the hormonal, sensory, and neural bases of rodent vocalization must be reexamined. For example, Geyer and Barfield (1978) found that ovariectomized female rats only emit ultrasounds if exposed to ovarian hormones; these and other results have led to the conclusion that "female-produced vocalizations were controlled by a hormone-sensitive mechanism" (Thomas & Barfield, 1985, p. 720). There may be, however, a more parsimonious explanation. Specifically, because hopping and other female sexual behaviors require the presence of ovarian hormones, and because hopping is associated with ultrasound emission, then any manipulation (e.g., ovariectomy) that decreases hopping may also indirectly decrease ultrasound emission.

Similarly, much work has been done on the affect of conspecific odors on ultrasound production. For example, gerbils emit ultrasounds when exposed to gerbil body hair (Thiessen, Graham, & Davenport, 1978). Given, however, the near-perfect correlation between activity levels and ultra-

sound production in this species, this effect of conspecific odor on ultrasound production may be the result of the odor's stimulatory effect on locomotion (Thiessen et al., 1978; Thiessen & Kittrell, 1979). Such an interpretation can be applied to similar findings in mice (Nyby, Wysocki, Whitney, Dizinno, & Schneider, 1979) and hamsters (Floody & Pfaff, 1977b).

Finally, sensitivity to the biomechanical basis of ultrasound production can lead to simplified hypotheses about a neural basis of ultrasound production. For example, Floody (1989) lesioned the ventromedial hypothalamus of female hamsters and found a decrease in the duration of lordosis and an increase in the rate of ultrasound production. Given an association between locomotion and ultrasound production in this species, this finding is to be expected: The less time the animal remains in the lordotic posture, the more time it has available to move about the cage and emit ultrasound. Floody did not, however, entertain this possible interpretation; instead, he concluded that the results "suggest a mechanism for the behavioral incompatibility of ultrasound production and lordosis. In particular, they raise the possibility that the suspension of ultrasonic calling that normally accompanies lordosis reflects an increase in [ventromedial hypothalamus] activity that simultaneously provokes lordosis and inhibits vocalization" (Floody, 1989, p. 299). Suggesting such a mechanism, however, is premature. Clearly, just as one need not hypothesize a neural basis for the incompatibility of sleeping and eating, one also need not hypothesize a neural basis for the incompatibility of lordosis and ultrasound emission, even if one assumes that a loose relation exists between ultrasound emission and locomotion.

Consequences for the Communicatory Significance of Ultrasound

If at least some ultrasonic emissions by gerbils and other rodents during behavioral arousal are acoustic by-products of biomechanical strain, then one can no longer speak of all these sounds as signals emitted in order to communicate. However, this does not preclude their communicating a useful message to conspecifics. In fact, as we have seen, there is good evidence that some rodent vocalizations do affect the behavior of conspecifics in predictable and useful ways. The point that must be stressed is that although these vocalizations do communicate a message, it is the receiver that determines the meaning of the vocalization. Thus, a female hamster can use ultrasound emission as a predictor of the presence and arousal of a nearby male (although female hamsters respond similarly to male and female vocalizations; Floody & Bauer, 1987), and one can argue that lengthening the retention of the lordotic posture is a beneficial response to such information. On the other hand, not all rodent vocalizations have clear communicatory effects, and we ought not to expect them to have such effects if some vocalizations are by-products of behavioral arousal and biomechanical strain.

It cannot be overemphasized that the effect of a vocalization is not necessarily identical to the function of the vocalization (Blumberg & Alberts, 1992). This distinction between function and effect is mirrored, in evolutionary theory, by the

terms *adaptation* and *exaptation* (Gould & Vrba, 1982; Williams, 1966). An adaptation is "any feature that promotes fitness and was built by selection for its current role" (Gould & Vrba, 1982, p. 6). Other characters, however, "evolved for other usages (or no function at all), and later [were] 'coopted' for their current role" (p. 6). Such characters, Gould and Vrba suggested, may be called *exaptations*. Thus, the operation of an adaptation is its function and the operation of an exaptation is its effect. With this framework, if a particular rodent vocalization is simply the incidental by-product of biomechanical strain, then it is not adapted for communication, regardless of its effect on conspecific behavior, because it was not selected for a communicatory effect. On the other hand, if conspecifics respond to this incidental vocalization in a way that is beneficial to the vocalizing animal, then the vocalization is exapted for communication.

Any ultrasonic vocalization can occur under one of the following circumstances. First, a vocalization can be emitted at will and under minimal constraints. In this instance, one can reasonably presume that the vocalization is part of a communicatory system in which the caller signals to a conspecific and effects a beneficial change in the conspecific's behavior. Such vocalizations are the best candidates for adaptations.

Second, a vocalization can be emitted as an acoustic by-product of other behaviors. For example, the audible grunting of human infants with respiratory distress syndrome is the acoustic by-product of laryngeal braking, as has been suggested for the ultrasonic distress call of rat pups (Blumberg & Alberts, 1990). In addition, as originally hypothesized by Thiessen and Kittrell (1979) and further argued in this article, some rodent ultrasounds may be acoustic by-products of thoracic compression during locomotion. If a vocalization is an unavoidable by-product of other bodily events, if the occurrence of the vocalization predicts a behavioral or physiological state in the caller, and if a conspecific can detect and react to the vocalization in a way that benefits the caller or the listener, then the vocalization is likely to generate the establishment of and become fixed within a communicatory system. Such vocalizations are the strongest candidates for exaptations. Furthermore, with time, the incidental vocalization can become ritualized and perhaps be emitted independently of other physical constraints.

Finally, a vocalization may be correlated with motor activity but not necessarily be an incidental by-product of motor activity. In such a case, the vocalization is a constrained adaptation; specifically, the mechanical linkage between the breathing cycle and locomotion (Bramble & Carrier, 1983) may necessitate that sound production be restricted to the time of expiration when the forelimbs are making contact with the ground. If this is the case, it is important to determine why locomotion and vocalization occur together if they are not causally linked. One possibility is that both are stimulated independently by a third variable, such as heightened arousal. A second possibility is that it is more energetically efficient to emit ultrasound during locomotion, when the mechanical energy is already available for sound production, than when stationary. Interestingly, with regard to this last possibility, it

has recently been demonstrated that the energetic cost of echolocation in bats is substantial at rest but negligible during flight (Speakman & Racey, 1991).

In practice, distinguishing between these possibilities may sometimes be difficult. Moreover, the problem becomes even more complicated when the dimension of learning is considered. Nonetheless, researchers can only benefit by attempting to draw these distinctions. Understanding the evolution of a communicatory system is an historical problem, and researchers must begin to develop greater sensitivity to the historical forces that can generate complex communicatory systems. It seems reasonable to expect that the evolution of some acoustic communicatory systems was driven by the advantageous use, by conspecifics, of information provided them by accident. This notion, that animals take advantage of latent information provided by conspecifics, is not new and can be found in the literature on chemical communication (e.g., Bryant & Atema, 1987).

Much work needs to be done to elucidate the relations between locomotion, respiration, and ultrasound production in rodents. Specifically, we need to monitor laryngeal activity and intratracheal pressure during ultrasound-related behaviors: If a particular ultrasonic vocalization is an acoustic by-product of thoracic strain during locomotion, then one may expect the larynx to constrict at about the time of the landing of the forepaws during locomotion and intratracheal pressure to increase as a result of thoracic compression. Sound production ought to occur as the larynx is blown open after maximum thoracic strain and maximum intratracheal pressure. Furthermore, it ought to be possible to manipulate the contribution of biomechanical factors to ultrasound production. For example, restricting the movements of animals or placing them on a surface that offers little mechanical resistance (in order to reduce reaction forces; this can be accomplished by testing animals on a soft, yielding surface) may decrease the emission of those vocalizations that are by-products of thoracic strain. Finally, future research needs to take into account the effects of experimental manipulations (e.g., hormonal treatments, brain lesions) on the activity and locomotor patterns of the animals. By focusing attention on the biomechanical bases of these vocalizations, researchers will begin to be able to distinguish between those vocalizations that are adaptations, those that are exaptations, and those that are neither.

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