

# Analysis of acoustic communication by ants

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An analysis is presented of acoustic communication by ants, based on near-field theory and on data obtained from the black imported fire ant *Solenopsis richteri* and other sources. Generally ant stridulatory sounds are barely audible, but they occur continuously in ant colonies. Because ants appear unresponsive to airborne sound, myrmecologists have concluded that stridulatory signals are transmitted through the substrate. However, transmission through the substrate is unlikely, for reasons given in the paper. Apparently ants communicate mainly through the air, and the acoustic receptors are hairlike sensilla on the antennae that respond to particle sound velocity. This may seem inconsistent with the fact that ants are unresponsive to airborne sound (on a scale of meters), but the inconsistency can be resolved if acoustic communication occurs within the near field, on a scale of about 100 mm. In the near field, the particle sound velocity is significantly enhanced and has a steep gradient. These features can be used to exclude extraneous sound, and to determine the direction and distance of a near-field source. Additionally, we observed that the tracheal air sacs of *S. richteri* can expand within the gaster, possibly amplifying the radiation of stridulatory sound. © 2000 Acoustical Society of America. [S0001-4966(00)04210-7]

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## INTRODUCTION

Many ant species, particularly those that live in the soil, communicate acoustically by stridulating.<sup>1</sup> Stridulation is the rubbing of one part of an insect's body against another to produce sound. The stridulatory organ of the black imported fire ant, *Solenopsis richteri*, described in the paper, is typical of ants. Amplified sounds of stridulation of *S. richteri* are provided on the internet.<sup>2</sup> Generally the sounds are barely audible. For *S. richteri*, they are just above a faint whisper, about 2 mPa or 40 dB (Ref. 20  $\mu$ Pa), at a distance of 100 mm.

The prevailing opinion among myrmecologists appears to be that acoustic communication is relatively unimportant compared to chemical communication.<sup>3,4</sup> In fact, it is believed<sup>4</sup> that ant communication evolved using chemicals, largely bypassing the use of sound. However, it is unlikely that acoustic communication is unimportant, in view of the number of species of ant that stridulate. Also it is unlikely that ants rely principally on chemical communication, because, in highly organized ant societies, it will frequently be necessary to update information. This cannot be done effectively with chemicals in the way that it can with sound.

The de-emphasizing of acoustic communication by myrmecologists appears to have resulted in some misunderstanding of the use of sound by ants, particularly with regard to the transmission and reception of stridulatory signals. It is easy to demonstrate by shouting at ants that they are unresponsive to airborne sound on a scale of a meter or more.

This was shown painstakingly for eight species of ants almost a century ago, using a piano, a violin, and a Galton whistle, over a frequency range from 30 Hz to 60 kHz.<sup>5</sup> On the other hand, because of the presence of subgenual chordotonal organs in the legs,<sup>4</sup> ants are sensitive to vibrations in the substrate. From this, myrmecologists have concluded that stridulatory signals are transmitted through the substrate.<sup>3,4</sup>

But an examination of the substrate-transmission hypothesis raises doubts about its validity. We can clearly hear ant signals transmitted through the air. Most recordings of ant signals reported in the literature are of airborne sound measured with sound pressure microphones. Other reasons for questioning the substrate-transmission hypothesis are discussed in the paper. It would seem that the stridulatory signals are principally airborne. Of course, ants must still be unresponsive to airborne sound on a scale of a meter or more. It is one of the purposes of this paper to show, from basic near-field theory, that ants can communicate through the air in the near field, on a scale of about 100 mm, and yet be insensitive to ambient airborne sound on a larger scale.

The receptors of airborne sound in ants are most probably trichoid, or hairlike, sensilla on the antennae. *S. richteri* and other ant species have concentrations of trichoid sensilla on the apical segments of the antennae. Many kinds of insects detect sound through the motion induced in trichoid sensilla by the particle velocity of sound, or sound velocity.<sup>6-8</sup> But, because of the belief in substrate transmission, this does not appear to have been considered for ants.

The overall objective of this paper is to develop a coherent understanding of acoustic communication by ants, based on near-field theory,<sup>9</sup> and on data obtained both from our investigation of *S. richteri* and from the work of others.

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Although the complete theory of the near field is not readily available in texts, it is well understood by entomologists that many species of insect sense sound velocity in the near field. What we have done is to show how ants can use the enhancement of sound velocity and the steep velocity gradient in the near field to improve the signal to noise ratio of stridulatory signals and to determine the location of small sources of sound.

*S. richteri* came to the United States from South America and is an example of an invasion insect which, when transplanted from its original habitat, can cause serious damage to animal and plant life. In the long run, the only way to control such insects is through basic research. Learning how they communicate acoustically is part of such research. First we provide some background information on *S. richteri*.

### BACKGROUND ON IMPORTED FIRE ANTS

There are two species of imported fire ant, *S. richteri* and *S. invicta*. The word “imported” distinguishes these ants from fire ants indigenous to the United States. In the 1930s, *S. richteri* was introduced accidentally from South America at Mobile, AL, followed by the more resilient red fire ant, *S. invicta*.<sup>10</sup> From Mobile, *S. invicta* spread throughout the Southeastern United States from Florida to Texas. Recently they became established in New Mexico and California.<sup>11</sup> *S. richteri* seem to exist principally in northern Mississippi and Alabama and in southern Tennessee<sup>10</sup> and were conveniently located for our study. The results we obtain for *S. richteri* apply equally to *S. invicta*. The density of imported fire ants in the United States is often about five times greater than in their original habitat in South America, apparently because there are no natural enemies in the United States, such as *Pseudacteon* phorid flies.<sup>11,12</sup>

The problem with imported fire ants is their sting. Each ant can sting many times and concerted attacks can involve thousands of ants. The stings are usually lethal to other insects, nestling birds, and young mammals. With humans, the stings can be painful; allergic reactions and sometimes death can occur.<sup>10</sup>

### THE STRIDULATORY ORGAN

As with many ant species, the stridulatory organ of *S. richteri* is located at the “waist,” i.e., at the junction of the postpetiole and the bulbous posterior portion of the abdomen, called the gaster (Fig. 1). It consists of a washboardlike set of ridges on the anterior dorsal surface of the gaster, together with a scraper on the rim of the postpetiole. When the gaster is moved up and down, the scraper is made to run back and forth over the file of ridges, generating squeaking sounds or chirps. The up and down movement of the gaster, sometimes called gaster flagging, is a visual indication of stridulation. The SEM (scanning electron micrograph) of the stridulatory organ of *S. richteri* in Fig. 2 shows the file of ridges on the gaster and the rim of the postpetiole containing the scraper. For *S. richteri*, the number of ridges is about 40 to 50. The frequency of the squeaking sounds appears to be determined largely by the rate of tooth impact of the scraper

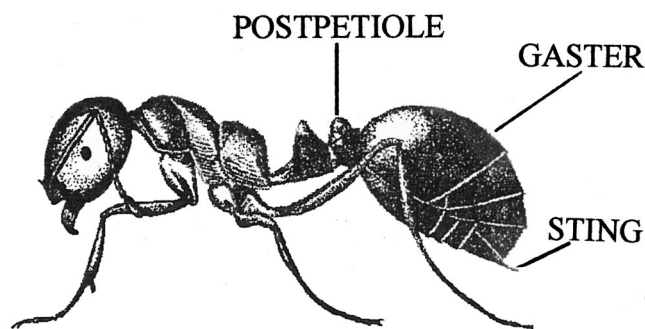


FIG. 1. Drawing of worker of imported fire ant, *Solenopsis richteri*. Typically, workers range in length from about 2 to 6 mm.

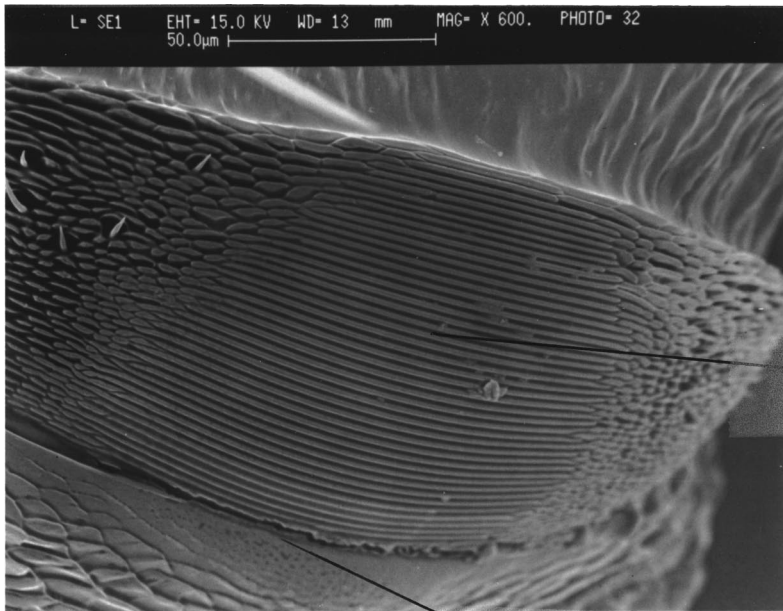
as it moves over the ridges.<sup>13</sup> LDV (Laser Doppler Vibrometer) studies of another ant species, *Atta sexdens*,<sup>14</sup> have shown that stridulatory sound is radiated principally by the surface of the gaster. Because the gaster is very small relative to the wavelength it seems unlikely that the sound is related to structural resonance. More probably it is caused by stick-slip<sup>15</sup> associated with frictional interaction between the scraper and the ridges.

*S. richteri* is unusual in that larger workers have a transparent dorsal cuticle on the gaster. This permits microscope examination of the expansion and contraction of the tracheal air sacs inside the gaster that are part of the respiratory system. A major worker of *S. richteri* was embrittled by dipping in liquid nitrogen and a portion of the gaster broken off to reveal the expanded sacs lying side-by-side, as shown in Fig. 3. It is seen that the expanded sacs fill the anterior of the gaster. Since they appear to be in contact with the outer cuticle, it is reasonable to suppose that they could play a role in amplifying the sound generated by the stridulatory organ. Microscope observation shows that the air sacs of *S. richteri* do not always expand when the ant is stridulating. Further investigation is needed to determine if there is a connection between the expanded sacs and stridulatory sound.

### STRIDULATORY SOUNDS

Examples of the stridulatory sounds of *S. richteri* were determined for different situations, as shown in Fig. 4. In this figure, the signals have an 8-s duration. Corresponding 24-s recordings of the signals are given on the internet.<sup>2</sup> The human ear can easily distinguish the sounds of stridulation from other sounds. Signal No. 1, in Fig. 4(a), is the sound generated by a large number of ants when a probe, fitted with a Bruel and Kjaer ½-in. microphone, is pushed into an ant mound. As the ants pass close to the microphone, a variety of different signals can be heard above the background noise of stridulatory sound. Clearly these are not “a monotonous series of chirps,” as described in Ref. 3. The ants appear to be highly agitated and they rush out to attack the probe. As has been noted previously by Wheeler,<sup>16</sup> the rapidity of the response is probably due to acoustic communication, because the reaction to chemical communication would be slower.

The variety of stridulatory sounds in the alarm signal induced us to perform additional tests in the laboratory. Part of an ant mound, in a plastic container about 250 mm in diameter and 100 mm high, was placed in a double sound-



**File of Ridges  
on Gaster**

FIG. 2. Scanning electron micrograph of the stridulatory organ of *S. richteri* showing the washboardlike set of ridges on the anterior dorsal surface of the gaster and the rim of the postpetiole containing the scraper.

**Scraper in Rim  
of Postpetiole**

proof box<sup>17</sup> with windows. Inside the box, the plastic container rests on a custom sensor consisting of a sensitive, low-cost electret microphone in a stethoscope head. This sensor has a sensitivity comparable to a 1-in. Bruel and Kjaer condenser microphone, i.e., about 50 mV/Pa. It has been used extensively to detect and monitor larval activity in cotton bolls, fruit, nuts and grain.<sup>17</sup> For ant sounds, this method of monitoring is similar to listening to sounds in an adjoining room with one's ear pressed against the wall. Both the ear and the microphone in the stethoscope detect sound pressure. Much of the signal processing was performed, for frequen-

cies up to 20 kHz, using a computerized speech-analysis system (Kay Elemetrics Model 4300).

Signal No. 2 in Fig. 4(b) shows the typical activity sounds of an undisturbed group of ants, punctuated briefly by chirps from an individual ant. The chirps occur at regular intervals. Their purpose is unclear, but they probably serve to indicate group or territorial awareness, one of the broad communication functions of social insects listed in Ref. 3. Signal No. 3 in Fig. 4(c) was generated by a single ant, during an attack on a caterpillar by a number of ants. This was the only type of stridulatory signal to occur during the attack. We also

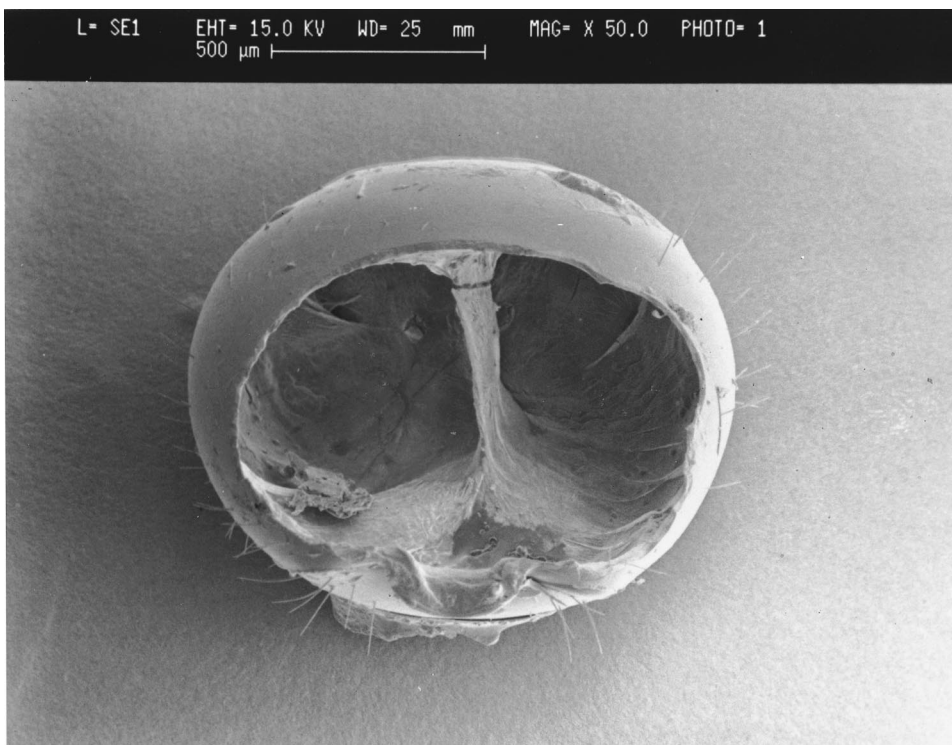


FIG. 3. Scanning electron micrograph of cryofractured gaster showing the expanded air sacs of a major worker of *S. richteri*.



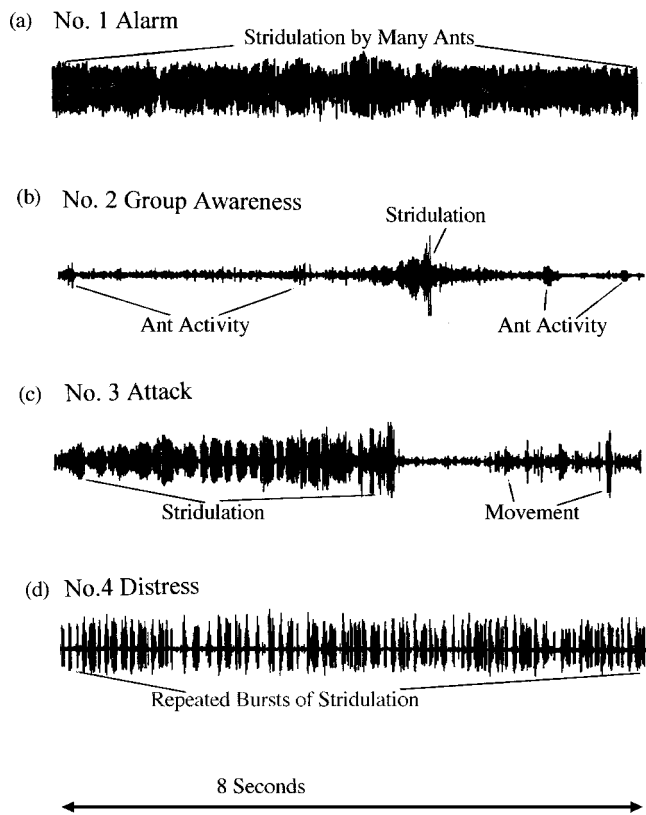


FIG. 4. Pressure-time traces of stridulatory signals of *S. richteri* (a) No. 1—Alarm signal due to insertion of microphone probe in mound; (b) No. 2—Sounds of normal activity with occasional stridulatory signal; (c) No. 3—Attack on caterpillar and (d) No. 4—Distress signal from ant with caught antenna.

recorded an attack on an earthworm, and struggles with other ants of the same species from a different colony. In these recordings, the stridulatory signals are the same as those in the attack on the caterpillar. The signal appears to come from a single ant. Whether this is always the same ant is unknown. The attack signal can also be heard among the stridulatory sounds in the alarm Signal No. 1.<sup>2</sup> Signal No. 4, in Fig. 4(d), was generated by a major worker with one of its antennae caught. This re-iterated type of distress signal was observed with both major and minor workers. In general the distress signal produced by majors is about 3 to 4 times louder than that of minors. Sometimes it is not as prolonged as in Fig. 4(d). There are other situations in which stridulation can occur, such as mating, moving the colony and in attacks by parasites, but these were not investigated.

One of the main differences between the signals in Fig. 4 is duration. Signal No. 1 lasts for about 10 min and then gradually dies away. Similarly signal No. 4 lasts for periods of minutes or more. Signals Nos. 2 and 3 are of much shorter duration. In addition, there appear to be other features that distinguish the signals from each other. The differences between the signals may indicate a kind of rudimentary language.

Since it was recorded with a B & K microphone with a flat response, the alarm Signal No. 1 was used to find the frequency spectrum of the sounds of *S. richteri*. The spectrum, shown in Fig. 5, was determined using MATLAB<sup>18</sup> with a digital filter to remove low-frequency ambient noise below

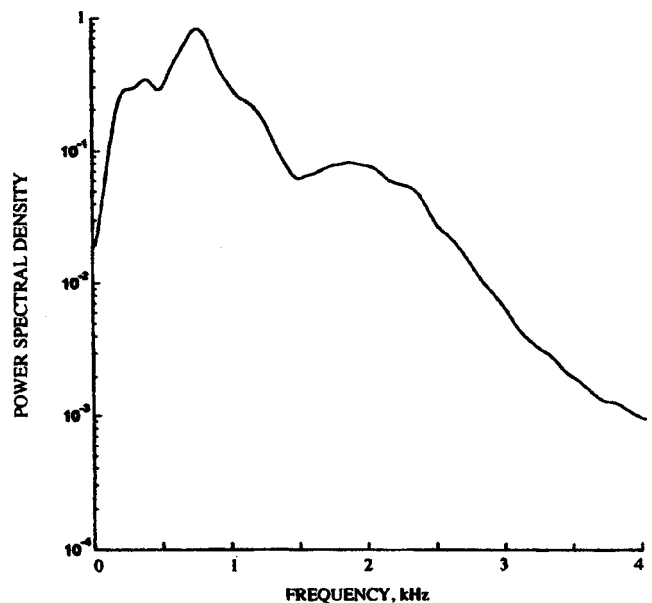


FIG. 5. Spectrum of alarm signal No.1 showing frequency content of stridulatory signals of *S. richteri*.

about 200 Hz. The peak of the spectrum is seen to occur around 700 Hz, with most of the spectral content below about 1.5 kHz. Stridulatory sound consists of unitary components, or syllables, associated with a single up-and-down movement of the gaster.<sup>19</sup> The ear can easily distinguish these, and they can be further identified from videos. Typically the duration of a component is less than three-tenths of a second.

## TRANSMISSION OF STRIDULATORY SOUND

The sounds of *S. richteri* are audible even when the ants are located on foam rubber. Hence it is reasonable to suppose that stridulatory signals are transmitted through the air. However, since there is a strong belief among myrmecologists that the signals are transmitted through the substrate, it is necessary to review arguments underlying this belief to examine their validity.

Evidence in support of the substrate-transmission hypothesis is believed to be provided by a well-known feature of ant behavior, namely the rescue, by fellow ants, of an ant buried beneath a soil subsidence. The buried ant stridulates (and emits chemical signals) to attract its fellows, and, since the stridulatory signals pass through the soil, this is taken to indicate that the signals are structure-borne through the substrate.<sup>3,4</sup> However, it is important to recall that soil is a granular, not a continuous solid. Sound transmission in granular materials is a well-studied field,<sup>20,21</sup> and one of the principal means of transmission is through the air in the inter-granular passages. This has been demonstrated, for example, by the differences in transmission speed that occur when the same granular material is immersed in different gases.<sup>22</sup> Also there are many kinds of insects that live (and breathe) in the soil. It would seem likely, then, that the acoustic signals of a buried ant are transmitted mainly through the inter-granular air passages and not through the

solid matrix of the soil. Certainly chemical signals are transmitted this way.

Evidence in support of the substrate-transmission hypothesis is also believed to be provided by the observation that an ant can excite structure-borne vibration in a leaf. The leaf-cutting ant, *Atta cephalotes*, stridulates and excites vibrations with its mandibles, as it cuts the leaf, apparently to attract other members of the colony to that particular leaf.<sup>23</sup> Using an LDV system, the vibrations of the leaf were found to be measurable when the mandibles of the stridulating ant are in contact with the leaf, but barely detectable when only the tarsi or feet are in contact.<sup>23</sup> When an ant stridulates, its mandibles generally are not in contact with the substrate. Since soil is not a continuous, flexible solid like a leaf, the vibrations caused by a stridulating ant through the tarsi are probably not detectable in soil. There are no known reports of LDV measurements of stridulatory vibrations in the soil. The structure of an ant's body indicates that it is not designed to transmit vibrations from the stridulatory organ to the substrate, because vibrations pass through the ant's body along a highly attenuating path, through various joints to tarsi with a very small contact area.

As they move about, ants are likely to encounter a variety of substrate materials, such as soil, wood, leaves, animal tissue and manmade objects of various sorts. Since these can have very different vibration characteristics, it is unlikely that ants have the ability to adjust acoustic communication accordingly. It is much more likely that ants use an unchanging, uncomplicated transmission path, through the air.

## RECEPTION OF STRIDULATORY SOUND BY ANTS

Since many types of insects use mechanosensory trichoid sensilla to detect airborne sound,<sup>6-8,24-32</sup> it is likely that ants do the same. Mechanosensory trichoid sensilla have membranous sockets and are free to move within a sound field. The sensilla are driven back and forth in the sound field by air-induced drag and virtual mass forces about the point of attachment.<sup>30,31</sup> They fire phasically in a one-to-one relation with direction during each cycle of oscillation. This sets an upper limit to the frequencies they can "hear" of about 1 or 2 kHz.<sup>6-8,24-32</sup> Trichoid sensilla occur on all parts of an ant's body. However, there are concentrations on the apical segments of the antennae, as shown in the SEMs of the antennae of *S. richteri* in Fig. 6. Similar concentrations occur with other ant species. For example, Dumpert counted 441 sensilla on the apical segments of *Lasius fuliginosus*.<sup>33</sup> Trichoid sensilla are used for olfactory, tactile and other forms of sensing, as well as for sound.

The segmented antenna of an ant is similar to that of some parasitic wasps and the honeybee in being elbowed between the long basal segment and the shorter terminal segments. The maneuverability provided at the antennal base and the elbowed joint allows the ant to hold the antenna straight, either laterally or anteriorly, or to hold the antenna with the basal segment forming a right angle with the terminal segments which may be directed anteriorly or ventrally.<sup>3,4</sup> The tips of the antennae can thus be aligned in any desired direction. This facilitates sensing the gradient of sound velocity in the near field. It allows the ant to orient the

antennae and extend the tips to obtain maximum sensitivity to the sound-velocity gradient and thus to determine the direction and location of a sound source. The distance between the extended tips of the antennae of a worker of *S. richteri* is roughly between 2 and 5 mm.

During the past two decades, there has been a major interest in the response of trichoid sensilla to sound.<sup>24-32</sup> The sensilla are particularly receptive to signals in the near field where the sound velocity is greatly enhanced. Sound velocity is a vector, in contrast to sound pressure, the scalar quantity commonly measured in acoustics. Sound velocity microphones have been developed for insect acoustics.<sup>34,35</sup> Also there are laser Doppler methods,<sup>36</sup> which have been used to measure gaster vibration<sup>15</sup> and the motion of trichoid sensilla.<sup>32</sup> However, it is difficult to use these methods in the restricted space of the near field. Instead the enhanced sound velocities of the near field have been simulated by intense plane sound waves, or with some form of relatively slow airflow.<sup>23-32</sup> In these simulations, an important feature of the near field has been neglected, namely the steep gradient of the sound velocity. The significance of the gradient is examined later, in the section on the use of near-field acoustics by ants.

## JUSTIFICATION OF THE MONOPOLE MODEL FOR ANT SOUNDS

The monopole model for ant sounds, given in the Appendix, shows how ants can use near-field sound for communication while excluding extraneous noise from further away. However it is necessary first to justify the model.

(a) *Frequency.* In the model, frequency has to be about a kilohertz or less because, when the frequency is greater than a few kilohertz, the near field is too small to include a sufficient number of ants for acoustic communication. Since the peak frequency in Fig. 6 occurs at about 700 Hz, *S. richteri* clearly meets this requirement. Similarly the peak frequency for other ant species is below a kilohertz, as, for example, for *A. sexdens*, in the spectrum in Fig. 3 of Ref. 14.

However, the stridulatory signals of the African ponerine ant *Megaponera foetens* (Fabr.),<sup>37</sup> and the leaf-cutting ant *Atta cephalotes* L.,<sup>38</sup> have been reported to be ultrasonic (above 20 kHz). If this is true, it presents a serious obstacle to use of the near field for acoustic communication. It is necessary, therefore, to examine these results carefully. The signal processing is the same in both papers. Stridulatory signals of airborne sound are given, but no spectral plots. By comparing the stridulatory signals with ultrasonic signals, say for a bat,<sup>39</sup> it is immediately seen that the stridulatory signals are not ultrasonic. Compared to the bat signals, the ant signals are significantly expanded in time, with respect to the peaks and zero crossings of the signals. Counting the peaks and zero crossings relative to the time scale provides an estimate of the center frequency of the signals.<sup>39</sup> This was found to be between 700 and 900 Hz, consistent with the peak frequency for *S. richteri* in Fig. 5. To be certain that there is no significant ultrasound in the signals, a more complete analysis was performed, digitizing the signals by hand and using MATLAB to generate a spectrum. Again this



(a)



(b)

FIG. 6. Scanning electron micrographs of the antenna of a worker of *S. richteri* showing (a) trichoid sensilla on the elbowed antenna and (b) concentration of trichoid sensilla on the apical segments.

showed a peak between 700 and 900 Hz, similar to Fig. 5. The conclusion that the signals are mainly ultrasonic thus appears to be a mistake.

To further demonstrate the absence of ultrasound in ant signals, we investigated the signals of *S. richteri*. We inserted a  $\frac{1}{4}$ -in. B & K microphone (Model No. 4135) into a

mount and analyzed the resulting sound using a Hewlett-Packard Model No. 35665A analyzer. This measurement system detects frequencies up to about 100 kHz. We found nothing significant above about 3 kHz.

In summary then, there appears to be no reason to believe that the frequency of ant signals occurs principally at



ultrasonic frequencies. Instead, the available evidence indicates that the frequency is mainly associated with tooth impact around and below 1 kHz, thus enabling ants to use the near field. It also follows that an ant is very small compared to the wavelength, which is another requirement of the monopole model.

(b) *Uniformity of Radiated Sound.* In the monopole model, it is assumed that the sound of the ant is radiated uniformly. To test the validity of this assumption, we used a Bruel & Kjaer  $\frac{1}{2}$ -in. microphone to measure the stridulatory sound from individual medium-sized workers of *S. richteri*, at different positions around the ant, at a radial distance of about 100 mm. The ants were restrained on a hard flat surface in an anechoic room and continuously emitted the distress signal No. 4. Because the signals varied with time, the sound field was never perfectly uniform. However, for all intents and purposes, it appeared to be uniform. We investigated the frequency range between 200 Hz and 1.6 kHz, looking in particular for the figure-eight pattern of a dipole, or for a pattern of null positions for a higher-order source. Nothing of this nature was found. The average overall rms sound pressure at 100 mm for *S. richteri* was found to be roughly 2 mPa (40 dB), or just above a whisper. This piece of data is used to further justify the model.

#### USE OF NEAR-FIELD SOUND BY ANTS

The sound velocity  $v$  corresponding to the sound pressure of 2 mPa for *S. richteri* measured at a distance of 100 mm, can be estimated using the simple formula for spherical waves relating pressure and velocity<sup>40</sup>

$$v = pF(kr)/\rho c, \quad (1)$$

where  $F(kr) = kr/\sqrt{1+(kr)^2}$ ,  $p$  is the sound pressure and  $\rho$  and  $c$  are the density and speed of sound of air. Equation (1) can also be obtained from Eqs. (A1) and (A2) in the Appendix. From Eq. (A6) in the Appendix,  $kr \sim 1$ ; hence  $v$  at 100 mm is  $3.1 \times 10^{-3}$  mm/s. From this it is possible to use the monopole model, at a frequency of 700 Hz, to extrapolate back to the velocity at the surface of the source (gaster), as shown in Fig. 7. We use 700 Hz because it is the frequency of the spectral peak in Fig. 5. Assuming the gaster of *S. richteri* to have a radius of about 1 mm, the extrapolated value of sound velocity at its surface is seen to be about 19 mm/s. The reasonableness of this result can be demonstrated by comparing with LDV measurements of the corresponding velocity at the surface of the gaster of *A. sexdens* at 1 kHz.<sup>14</sup> Measurements at four locations on the gaster (Table I in Ref. 14) were converted to ordinary units and arithmetically averaged, resulting in a value of 30 mm/s, which is compared to the extrapolated value of 19 mm/s for *S. richteri*. The comparison cannot be expected to show close agreement, but it is close enough to show that the monopole model provides a realistic representation of the enhancement and steep gradient of the sound velocity in the near field of an ant.

How the steep gradient of the sound velocity affects the response of trichoid sensilla has not been investigated. It is likely that the sensilla will respond more sensitively in the steep gradient than with plane waves. The study of such an effect is beyond the scope of this paper. What can be done

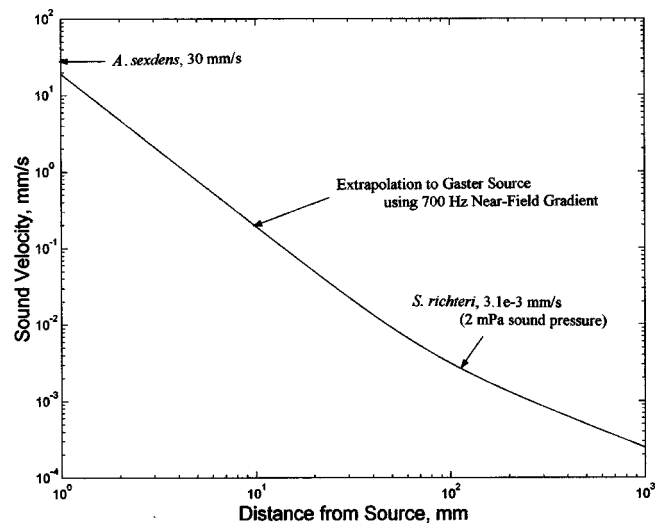


FIG. 7. Gradient of the sound velocity in the vicinity of a small spherical source of 1 mm radius, pulsating at a frequency of 700 Hz. This shows the extrapolation back to the source from a sound velocity of  $4.4 \times 10^{-3}$  mm/s at 100 mm for *S. richteri* (corresponding to a sound pressure of 2 mPa), compared to the velocity at the surface of the gaster for *A. sexdens* (Ref. 14).

here is to investigate the use of the two antennae of an ant to sense the steepness of the gradient, using relative differences in sound velocity between the antennae. We assume two separations of the tips of the antennae, 2 and 5 mm apart, and calculate the relative difference in sound velocity between the tips, using the data in the 700 Hz curve in Fig. 7. The difference in percent is plotted in Fig. 8, as a function of distance from the source. The figure shows how, by using the antennae to sense the relative difference in sound velocity, an ant can be sensitive to sound in the near field of a small source but insensitive to sound in the far field. In the near field, the difference is greater than 10%, which is a threshold often found by experimental psychologists to be the just noticeable difference in sensation between two sensors. For example, the threshold for detecting interaural sound-pressure differences in human hearing is 6%–10%.<sup>41</sup> On the other hand, in the far field, the relative difference in sound velocity

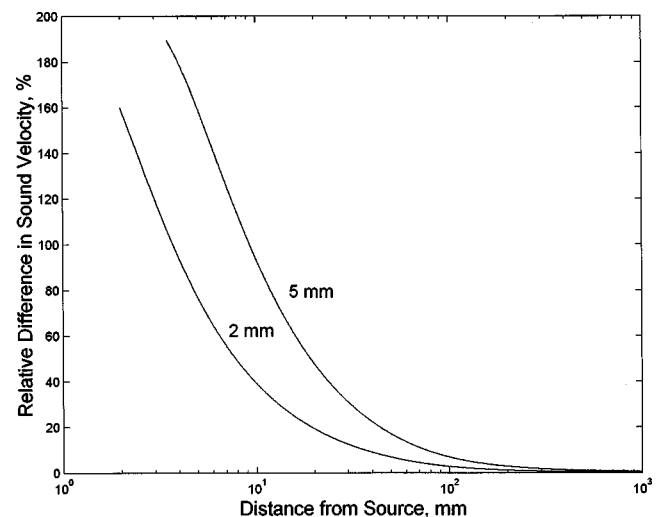


FIG. 8. Percent relative difference in sound velocity between the tips of the antennae of *S. richteri*, 2 and 5 mm apart, for the velocity gradient in Fig. 7.

is vanishingly small, well below the 10% threshold. The steep gradient thus creates a special condition, which enables an ant to sense signals from another ant, while shutting out extraneous noise interference.

In summary, the two features of the near field that can be used to improve the signal to noise ratio of ant signals are (a) the enhancement and (b) the steep gradient of the sound velocity. Since the stridulatory signals are quite distinctive, it is possible that ants may also use simple signal processing. The near field thus provides ants with an acoustical world of their own. It is conjectured that ants can extend the range of acoustic communication beyond the near field by relaying signals from one to another. Also it is conjectured that the larger ants of *S. richteri* play a greater role in acoustic communication than the smaller ants.

In Fig. 8 it is assumed that the tips of the antennae are in line with the small source. This orientation is the most sensitive for detecting relative differences in sound velocity. Because of the maneuverability of the antennae, an ant can always adjust its antennae to this position, thus determining the direction of the source. Figure 8 also shows there is a one-to-one relation between the relative difference in sound velocity and the distance to the source. This provides a means of determining the distance to the source, as well as its direction. Since ants appear to have poor vision<sup>3,4</sup> and often operate in the dark, this capability would be quite useful.

The monopole model in the Appendix is for a small pulsating spherical source in free space. However, in the environment of an ant, there are reflecting surfaces. If the ant is resting on a reflecting planar surface, the model continues to provide a realistic representation of the near field. But, inside a mound, the walls of tunnels and galleries form different kinds of reflecting surfaces, which require more complex modeling. The enhancement and steep gradient of the sound velocity still occur in the near field, however.

## INTERACTION WITH PHORID FLIES

It is known that fire ants can detect phorid-fly parasites as they hover a few millimeters above the ants.<sup>12</sup> Presumably they detect the sound of the fly's wing beats. This provides an additional argument for believing that ants sense sound through the air. The frequency of the wing beats of the phorid fly has not been measured, so that the corresponding extent of its near field is not known.

## CONCLUDING COMMENTS

That ants communicate through the air in the near field appears to be the only consistent way of explaining the facts relating to acoustic communication by ants. There is as yet no direct experimental proof that ants sense the relative difference in sound velocity between the antennae, but they are capable of it and, in view of the advantages it provides, it would be surprising if they did not. The near field of a small source with its enhancement and steep gradient of the sound velocity are major features in the acoustic environment of ants. In fact, it seems likely that the ants' stridulatory and acoustic sensing systems have evolved by making use of

these features. As indicated in the Appendix, ants use lower frequencies to increase the range of the near field, even though this reduces the power of the radiated sound. Hence they have to rely on the features of the near field to improve the signal to noise ratio of their signals. It is likely that other insects make similar use of the near field.

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## APPENDIX

The complete theory of a monopole, or simple source, is not generally available in texts. We use the theory given in Ref. 9. It is also available in some older texts, for example, Ref. 42.

A monopole radiates sound equally in all directions. It can be represented by a small sphere of radius  $a$  located at the origin, pulsating periodically with circular frequency  $2\pi f = kc$ ,  $f$  being the frequency,  $k$  the wave number and  $c$  the speed of sound in the fluid medium. The pulsations of the monopole have a volume rate of fluid flow  $S$ . At a radial distance  $r$  in the surrounding acoustic field, the sound pressure  $p$ , and the radial sound velocity (particle velocity of sound)  $v$  are given respectively by

$$p = -\rho c^2 ika(a/r)G, \quad (A1)$$

$$v = -c(a/r)^2 [ika(r/a) - 1]G, \quad (A2)$$

where  $G = S \exp[ik(r-ct)]/(4\pi a^2 c)$  and  $i$  is the square root of  $-1$ . To draw conclusions from these equations for different frequencies, source sizes and fluid media, it is helpful to introduce nondimensionalization as follows:

$$S' = S/(4\pi a^2 c); \quad p' = p/(\rho c^2); \quad v' = v/c \quad \text{and} \quad r' = r/a, \quad (A3)$$

together with the nondimensional frequency parameter  $ka$ . The amplitudes of  $p'$  and  $v'$  are then

$$|p'| = ka(1/r')S' \quad (A4)$$

and

$$|v'| = (1/r')^2 [1 + (ka r')^2]^{1/2} S'. \quad (A5)$$

The sound velocity varies as  $1/r'^2$  close to the source and as  $1/r'$  further away. The region of  $1/r'^2$  dependence is called the near field and the region of  $1/r'$  dependence is called the far field. The near field gradually merges into the far field. Unlike sound velocity, sound pressure varies as  $1/r'$  in both the near and far fields. Thus sound velocity characterizes the near field, not sound pressure. The near field consists of a nonpropagating reactive energy field, which forms a transition zone between the relatively high velocity of the radiating surface of the source and the much lower sound velocity of normal acoustic propagation in the far field.<sup>9</sup> The change



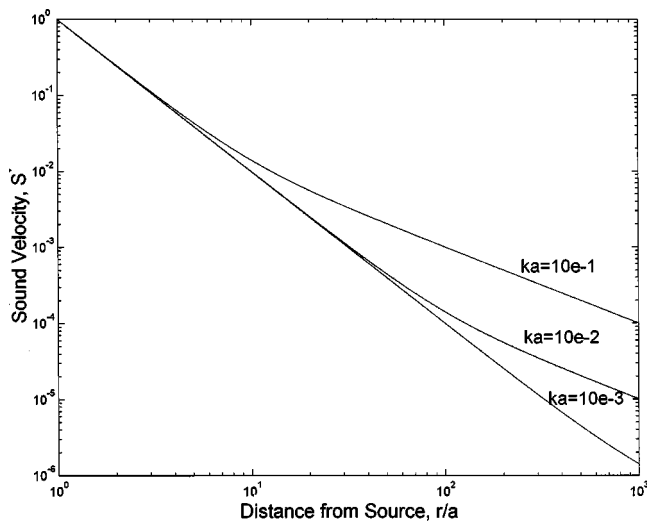


FIG. A1. Gradient of the sound velocity amplitude for different values of the nondimensional frequency  $ka$ , for a small pulsating sphere of radius  $a$ , showing the near and far fields, plotted as a function of the nondimensional distance  $r/a$  from the surface of the sphere.

in slope is illustrated in Fig. A1 where the amplitude of  $v'$  is plotted as a function of  $r'$  for different values of  $ka$ . From the figure, it is seen that the change occurs roughly when  $kar' \sim 1$ , or more simply when

$$kr \sim 1. \quad (\text{A6})$$

This relation determines the extent of the near field, given the frequency of the sound and the nature of the fluid medium. The lower the frequency the greater the extent of the near field. For example, if the frequency is 700 Hz, the corresponding wavelength in air is about 0.5 m. From the relation  $k = 2\pi/\lambda$ , where  $\lambda$  is the wavelength, it follows that  $k$  is about  $12.7 \text{ m}^{-1}$ . From Eq. (A6) the radial extent of the near field is then approximately 80 mm.

The driving force DF at the surface of the small spherical source is given<sup>9</sup> by

$$\text{DF} = -i4\pi a^2 \rho c^2 k a S' \exp[ik(r-ct)], \quad (\text{A7})$$

which increases linearly with frequency. The radiated sound power RSP is

$$\text{RSP} = \rho c 4\pi a^2 (ka)^2 S'^2, \quad (\text{A8})$$

which increases as frequency squared. An ant can thus increase the power of the sound it radiates by increasing the frequency. However, this reduces the size of the near field and increases the driving force or effort expended by the ant. Apparently ants have opted for greater range with less effort and hence rely on the special features of the near field to improve the signal to noise ratio of stridulatory signals. In water ( $c = 1500 \text{ m/s}$ ), the extent of the near field is about four times greater than in air ( $c = 344 \text{ m/s}$ ).

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