

# Ants are deaf

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Workers of a number of ant species produce vibrational signals, a phenomenon called “stridulation,” with a specialized organ located on their gasters. Even though stridulation can be heard by humans as faint air-borne sound, it has repeatedly been shown that ants are insensitive to the air-borne components of such signals. Instead, they are highly responsive to their substrate-borne components. Contrary to this view, it has recently been claimed that fire ants can hear stridulatory signals produced by nest mates as near-field sound, and that there is no evidence of signal transmission through the substrate in ants. In the present letter, this view is challenged by calculating the amplitude of the near-field particle oscillation around a stridulating ant, and by comparing it with the sensitivity threshold of the ant sensory receptors. The amplitude is shown to be at least 50 times lower than the sensitivity threshold, a fact that precludes the perception of the signals with the stiff antennal sensilla (and Johnston organ) so far described for ants. Finally, published data and our own findings on vibrational communication in ants are summarized, clearly showing that they are highly responsive to the substrate-borne components of stridulatory signals, and insensitive to near-field sound. © 2001 Acoustical Society of America.

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In the October issue of *JASA*, Hickling and Brown claimed, based on theoretical considerations and empirical data they obtained from work with fire ants, that ants can hear stridulatory signals produced by nest mates as near-field sound (Hickling and Brown, 2000). Moreover, they argued that communication via substrate-borne vibrations in ants is unlikely and that there is no evidence for ant responses to the substrate-borne components of vibrational signals (stridulation), maintaining that “there is a strong belief among myrmecologists that the signals are transmitted through the substrate” (Hickling and Brown, 2000, p. 1923). In our opinion, the authors’ arguments contradict all previous communication-behavioral experiments in ants, and also disagree with published studies on sensory physiology of insect receptor sensilla which are relevant for the issues being discussed.

We do not intend here to review the bulk of literature on ant vibrational communication, but merely point out some aspects that indicate that ants are insensitive to air-borne sound. That ants are highly sensitive to substrate-borne vibrations in the absence of air-borne sound was demonstrated as early as 1936 by Autrum, who was able to separate the effects of sound and substrate vibration on ant responses in a series of clear-cut designed experiments.

But what about the ant responses to sound in the absence of substrate-borne vibrations? Hearing is based on the reception of either sound pressure or the oscillation of air particles around a sound source. Sound pressure is received by ear drums, particle oscillation by highly moveable levers, both linked to mechanosensory neurons. Indeed, some ant species

can produce sounds by a process called stridulation in which a series of cuticular edges are rubbed against a scraper (Markl, 1968). Ants have no ear drums; when exposed to a standing sound wave the ants do not show any behavioral reaction in the sound pressure maxima. However, they exhibit behavioral reactions at positions in which particle oscillation is maximal (Autrum, 1936). At first glance this seems to support the recent published claim that ants can hear (Hickling and Brown, 2000), yet a closer inspection of the physical and physiological circumstances shows this to be incorrect.

The air particle oscillation around a sound field is the so-called near field. The strength and the spatial structure of this near field depends on the size of the sound source, on the mode of sound generation (monopole, dipole), and on the sound frequency produced. The most effective near-field sound source is a so-called monopole, i.e., a pulsating sphere. Based on measurements of the sound pressure generated by a stridulating *Solenopsis* fire ant, which averaged 2 mPa, Hickling and Brown (2000) calculated the particle velocity at 100 mm of the ant gaster as being  $3.1 \times 10^{-3}$  mm/s (their Fig. 7). They hypothesized that the steep gradient of the particle velocity around the source would affect the response of the trichoidea sensilla on the ant antennae, which were supposed to be the structures responsible for sound perception, and they even discussed on theoretical grounds the possibility that ants use the relative differences in sound velocity between both antennae to sense the steepness of the sound gradient.

Their arguments, however, overlooked the *amplitude* of the particle oscillation around the stridulating ant, and, also, to what extent the generated particle oscillation amplitudes match the sensitivity threshold of the sensory receptors so far

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studied in ants. To evaluate Hickling and Brown's arguments, we use their data on *Solenopsis* fire ants for our calculation of the amplitudes of the particle oscillation around a stridulating ant: basic stridulation frequency: 700 Hz; size of the ant gaster: 1 mm radius. For the calculations of the particle displacement amplitudes in the near field of an ant we also assume the ant gaster ("abdomen") to behave as a monopole during signal production, simply because if the data show for a monopole that the stimulus is too weak to be detected by the ants, then it must be true for all higher-order sound sources.

Any sound source has the properties of a monopole as long as  $k \cdot a_0 < 1$  ( $k = 2\pi/\lambda$ ,  $a_0$  = radius of sound source,  $\lambda$  = wavelength). Taking for the ant gaster (from where the sound is being radiated) a radius of 1 mm, and  $\lambda$  being 300 mm at 1 kHz, the conditions for a monopole are fulfilled. The near-field particle displacement amplitude drops from a zeroth-order sound source with increasing distance following  $1/r^2$  ( $r$  = distance to the center of the sphere); from a first-order sound source with  $1/r^3$ , etc. The near-field particle displacement amplitude ( $d$ ) for a zeroth-order sound source can be calculated according to

$$d = a_0^2 \cdot \Delta d / r^2 \quad (F1)$$

(where  $\Delta d$  = displacement amplitude of the surface of the sphere).

For the amplitude of the oscillation at the gaster surface (i.e., the amplitude resulting from a pulsating movement of a sphere at 700 Hz), which represents the *particle displacement amplitude (pda)*, we take 4  $\mu\text{m}$  as measured for *Atta* leaf-cutting ants (Masters *et al.*, 1983), even though the gaster of *Solenopsis* ants has a volume about six to eight times smaller than that of leaf-cutting ants, so that the value likely represents an overestimate.

According to F1 we calculate a  $pda = 2 \mu\text{m}$  at 1 mm, 0.04  $\mu\text{m}$  at 10 mm, and 0.0004  $\mu\text{m}$  at 100 mm distance from the stridulating ant. Using the data reported by Hickling and Brown (2000), i.e., a particle velocity of 3.1  $\mu\text{m/s}$  generated by a stridulating *Solenopsis* ant at 100 mm, we obtained a  $pda = 0.0007 \mu\text{m}$ .

Do ants possess sensory receptors which can detect stimuli of such low amplitudes? Near-field receptors so far described and analyzed in insects are sensory hairs or antennae. Both are connected to sensory neurons and function as levers driven by the air oscillation. Specialized mechanosensory hairs are extremely sensitive to slightest air movements. The most sensitive arthropod hairs known were described in spiders, caterpillars, and the cercal system of crickets (Barth, 2000; Kumagai *et al.*, 1998; Tautz, 1977).

With regard to ants, such high-sensitive mechanosensory hairs, which would be physically responsive to slight air movements in a sound field, have not been detected in any species investigated so far. All ant mechanoreceptor hairs are stiff contact sensilla, morphologically different from the mechanosensory hairs mentioned earlier (Dumpert, 1972).

How about the antennae as a whole? In the joint between the pedicel and flagellum of the antenna the so-called Johnston organ is located, a structure composed of up to several hundred of mechanosensory cells responding to

movement of antennal flagellum. While a recent paper reported an extremely high sensitivity for the mosquito antenna, lying in the nanometer range of air particle displacement in the sound field (Göpfert and Robert, 2000), behavioral experiments in ants showed that sound intensities starting from 100 dB (corresponding to displacement amplitudes of the air particles of 2  $\mu\text{m}$  at 810 Hz) can oscillate the antennal flagellum, evoking ant behavioral responses (Autrum, 1936). However, these values are 50 times greater than any sound field ants are able to generate as short as in 10 mm distance. Ants did not respond to sounds of lower intensities. Taking all these insights together, it is not surprising that no one has discovered behavioral reactions in ants to physiologically relevant sound stimuli.

How do ants perceive stridulatory signals? Stridulatory vibrations are transmitted from the ant body to the substratum (and they are surrounded by or vegetation they stand on). The energy is traveling as substrate vibrations from sender to receiver, eliciting a particular response or influencing their probability of occurrence. This has been demonstrated using several different experimental designs (Markl, 1965, 1967; Markl and Hölldobler, 1978; Baroni Urbani *et al.*, 1988; Rocés *et al.*, 1993). In the case of foraging leaf-cutting ants, the production of stridulatory vibrations correlates with the actual mandibular movements during leaf-cutting, so that most of the energy is led into the substrate through the mandibles (Tautz *et al.*, 1995). In fact, play-back experiments clearly showed that ants responded to the substrate-borne signals (Rocés *et al.*, 1993). With regard to signal perception, insects possess so-called subgenual organs (SGO), highly sensitive mechanoreceptors that respond to substrate vibrations. In electrophysiological experiments, it was shown for leaf-cutting ants that the SGOs respond to substrate vibrations produced by ant stridulatory signals (Markl, 1970).

In sum, ant stridulation can be heard by humans as faint air-borne sound, but cannot be detected by ants either as sound pressure or as particle oscillation. However, if the energy is sent through the substrate, ants are not only sensitive to the signal, but also show particular, even context-specific, reactions (Rocés and Hölldobler, 1995).

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