

# Reception of Particle Oscillation in a Medium – An Unorthodox Sensory Capacity

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The oscillation of particles in a medium is the adequate stimulus for specialized receptors. Such receptors can be found in nearly all phyla in the animal kingdom. Specialized sensory hairs in arthropods are used here as an example to show conditions and limits of vibration reception in a medium. The use of this sensory capacity in biologically relevant situations is shown on some well-known examples.

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The typical distance senses of animals are vision, olfaction, hearing and vibration reception. A special case of hearing and vibration reception is the detection of the oscillation of medium particles in a sound field. Since this sensory capacity is much less well known than "hearing" in its usual sense (reception of pressure variation in a medium [1]) its physiological and physical characteristics are considered here in detail.

Medium particles near a source of disturbance in an elastic medium are displaced and transmit this displacement to neighboring particles. The disturbance is thus propagated as a pressure variation (variation of the packing density of the molecules) through the medium. Pressure variation and particle displacement are therefore strictly connected: pressure variation cannot occur without particle displacement. It is possible to distinguish between particle oscillation and pressure variation by using different recording systems [2, 3]. A simple pressure-sensitive transducer consists of an air-filled chamber with massive walls, one of which is easily moveable by the pressure variations. Since pressure is a scalar quantity, the orientation of the chamber in the sound field is unimportant as long as the pressure across the diaphragm is uniform, i.e., as long as the chamber is small in comparison with wavelength. By contrast, a dis-

placement receiver must not be an obstacle in the sound field; it should be small and easily moveable so that it can faithfully follow the oscillation of the medium particles. Since particle oscillation is a vector, a displacement receiver can have a directional characteristic of sensitivity, i.e., its response can depend on its orientation in the sound field.

Both pressure variation and particle oscillation can be used by animals for detecting and localizing a sound source although the two parameters are not equally appropriate in every situation. The efficiency of a sound source in radiating sound pressure depends on the amplitude of vibration and on the relation of size of the vibrating structure and the wavelength of the produced sound. From the simplest sound source, a pulsating sphere (monopole, zero-order sound source) sound with a wavelength longer than 6 times the radius of the sphere is very poorly radiated [4].

Let us now consider a very common type of sound source: Flying insects often produce sound by their wingbeat. Although actually radiating as a dipole [5] an insect – e.g., a wasp – with 2 cm winglength can be approximately treated like a monopole with 2 cm radius for frequencies up to nearly 3 kHz, which includes the characteristic wingbeat frequencies of nearly all insects (for explanation see [4–6]). However, the lower frequency limit for efficient sound-pressure radiation for a source of this size is ca. 2900 Hz (wavelength =  $2 \cdot 6 = 12$  cm). Therefore, this insect is an extremely poor sound-pressure radiator. On the other side, air-particle displacement in the vicinity of the flying insect can reach remarkably large amplitudes (see below: Near Field) that is easily perceived by receptors sensitive to this kind of mechanical stimulation.

Although this article concentrates mainly on medium-vibration reception by arthropods, this sen-

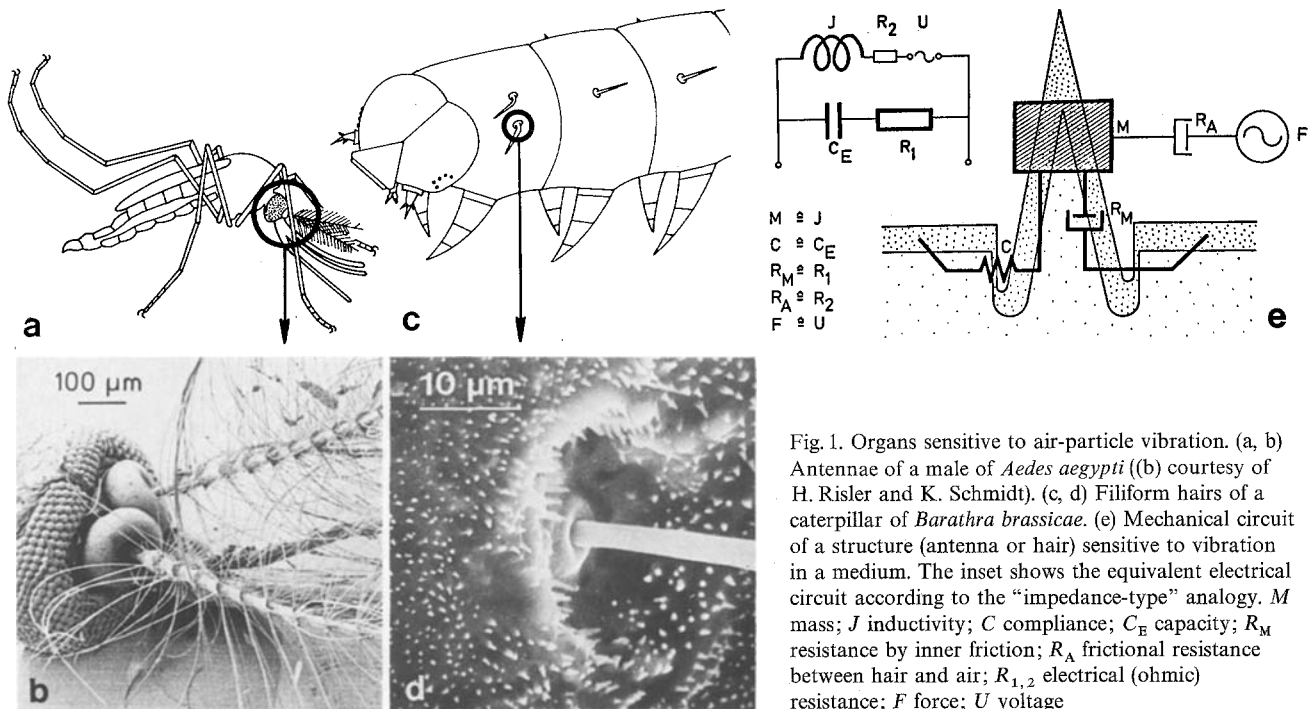


Fig. 1. Organs sensitive to air-particle vibration. (a, b) Antennae of a male of *Aedes aegypti* ((b) courtesy of H. Risler and K. Schmidt). (c, d) Filiform hairs of a caterpillar of *Barathra brassicae*. (e) Mechanical circuit of a structure (antenna or hair) sensitive to vibration in a medium. The inset shows the equivalent electrical circuit according to the "impedance-type" analogy.  $M$  mass;  $J$  inductivity;  $C$  compliance;  $C_E$  capacity;  $R_M$  resistance by inner friction;  $R_A$  frictional resistance between hair and air;  $R_{1,2}$  electrical (ohmic) resistance;  $F$  force;  $U$  voltage

sory capacity is also found in many other animals, and the following physical considerations apply to them – mutatis mutandis – as well.

Arthropods use sensory hairs or antennae for detecting particle vibration in a medium (Fig. 1). Sensory hairs are the most common and best-analyzed type of mechanoreceptors in arthropods. They consist of the hair shaft, its articulating membrane, and one or more sensory cells attached to the hair base. Modifications of the mechanical properties of the hair and of the response characteristics of its sensory cell(s) result in sensory specializations, making the hairs either sensitive to contact ("tactile hairs") or to motion of the surrounding medium, which can be unidirectional flow or rhythmic oscillation. It is obvious that hairs that can be stimulated by medium oscillation can in principle also respond to unidirectional flow and vice versa if the stimuli are strong enough and if the transfer function of the system is neither purely phasic nor purely tonic. So it is not surprising that the same sensory hairs have been described either as air-flow receptors or as "hearing organs" (e.g., head hairs in honeybees [7, 8]).

Displacement reception in water is for *vertebrates* an important sensory capacity. Fishes and amphibians receive water displacement through their lateral-line system. The ciliary processes projecting from the apical end of the sensory cells (neuromasts) are covered by a gelatinous cupula which is moved by water displacement. Investigations of the structure

and motion of the cupula of the lateral-line system in *Necturus maculosus* have shown that the cupula moves approximately like a rigid body [9–12]. This fact, and the dimensions of the cupulae (slender cylindrical bodies, ca. 40 µm in diameter and 200–800 µm long), allows use of the formulae that are given for sensory hairs in air. In more complicated lateral-line organs where the cupulae are flat sheets or standing in canals, the description of the mechanical processes is more complicated. The same is true for hair displacement in the vertebrate labyrinth.

In order to understand the physical constraints under which medium-vibration receptors are working one has first to consider the characteristics of waves in elastic media.

### Vibrations within Elastic Media

#### Air

Air is a mixture of elementary gases, but it has rather homogeneous physical properties. Parameters of interest in the present context are its density  $\rho$  and viscosity  $\eta$ . Both determine the mode and the velocity of the transmission of a disturbance through air. At sea level (static pressure =  $1.013 \cdot 10^5$  mbar) and 15°C  $\rho = 1.225$  kg/m<sup>3</sup>,  $\eta = 1.7894 \cdot 10^{-5}$  N·s/m<sup>2</sup>. Both decrease with increasing altitude, falling barometric pressure and temperature. Sound propagation velocity  $c$  in air is 340.29 m/s at 15°C and at sea level (for dependence of sound-propagation velocity on the humidity of air, see [13]). It is related to the wavelength  $\lambda$  of the sound at a given frequency  $f$  according

$$c = \lambda \cdot f. \quad (1)$$

In a sound wave the air particles don't travel through the medium; they oscillate around their resting position. The vector of this oscillation is oriented in the direction of propagation of the pressure wave. This oscillation can be described by its frequency and the amplitude of either the displacement, velocity or acceleration of the particles.

#### Water

All considerations and formulae reported for air apply also for periodic disturbances in water. The higher density of water (999.13 kg/m<sup>3</sup> at 15°C) results in ca. 5 times higher sound-propagation velocity ( $c=1466.25$  m/s at 15°C) and thus in ca. 5 times longer wavelength at a given frequency. How the propagation velocity of sound in water, and thus the wavelength at a given frequency, depend on temperature and density is given in [13]; how it depends on salt content is shown in [14].

For the characteristics of water-surface waves which are also produced by particle displacements see [6, 15–18].

#### Near Field and Far Field

In describing the radiation of sound from a source it is important to distinguish between near-field and far-field conditions. It was shown that pressure variation is always caused by particle displacement. On the other hand, particle displacement does not always cause pressure variation. In the vicinity of an oscillating object large particle displacements can take place that cause no energy transport over distance and thus no pressure variation – depending on the frequency of oscillation and the size of the source. This so-called near-field oscillation is generated because a definite volume of the surrounding medium streams around the sound source rather than being compressed by it (for more detailed description see [4]). For a monopole the amplitude of this near-field displacement decreases with  $1/r^2$  ( $r$ =distance from the sound source), for a dipole by  $1/r^3$  [19]. On the other hand, the particle displacement that causes the propagated pressure variation (“far-field displacement” because it dominates at greater distance from the source) decreases for every type of sound source with  $1/r$  resulting in the well known inverse square law of sound intensity. In practice far-field attenuation in air is also influenced by atmospheric conditions, like humidity [20]. For a monopole near field and far field are equal at a distance  $r=\lambda/2\pi\approx\lambda/6$  from the surface of the sound source. The near-field displacement can be completely neglected at distances  $r>\lambda/2$  [21]. This is also true for higher-order sound sources if they hold  $k\cdot a_0<1$  ( $k=2\pi/\lambda$ ,  $a_0$ =radius of sound source) because then the near field is dominated by the zero-order component of the sound source, i.e., it can be treated like a monopole. In the far field the maximum particle velocity  $v$  and the amplitude of particle displacement  $\xi_F$  can be calculated from the easily measurable peak amplitude  $p$  of sound pressure according to

$$v = p/\rho \cdot c \quad (2)$$

and

$$\xi_F = p/\rho \cdot c \cdot 2 \cdot \pi \cdot f. \quad (3)$$

At distances  $r<\lambda/2$  the near-field displacement must be taken into consideration. The near-field oscillation lags the far-field oscillation (which causes the sound pressure) by  $\pi/2$ . Near-field and far-field particle displacement must thus be added vectorily in order to get the real particle displacement in any particular place. If it is not possible to measure the resulting particle displacement  $\xi$  at distances  $r\leq\lambda/2$  from a source directly, it can be calculated from the measured sound pressure according to

$$\xi = \frac{\xi_F}{\cos \gamma} \quad (4)$$

( $\gamma$ =phase angle between  $\xi_F$  and  $\xi$ ,  $\tan \gamma=1/k \cdot r$  [22]). For the treatment of higher-order sound sources see [4, 19].

In water are the longer wavelengths responsible for the fact that the near-field effects spread ca. 5 times farther than in air. However, the amplitude of particle displacement in the far field of a sound source is about 3 500 times smaller in water than in air (see Eq. 3) for the same value of sound pressure.

## Physical Constraints and Physiological Characteristics of Medium-Oscillation Reception by Sensory Hairs

### The Driving Force

As pointed out, the stimulating parameter for mechanoreceptive hairs is particle oscillation, not pressure variation. This, however, does not yet answer the question whether the hairs' motion is driven by viscous force, inertial force, or both forces together. It was impossible to decide this by measuring the resonance characteristics of the displacement-sensitive hairs of caterpillars [22]. This problem can, however, be solved theoretically for a “floating sphere” that is forced to oscillations in a sound field. For every sphere diameter there exists a limiting frequency between a lower frequency range where viscous forces drive the sphere and a higher frequency range where inertial forces dominate [4]. E.g., for a sphere with a diameter of 200  $\mu\text{m}$  this frequency limit is 180 Hz in air.

In the case of a sensory hair these two frequency ranges must also exist but it is not quite clear which frequency separates the ranges. According to theoretical considerations of Stokes [23] a typical arthropod sensory hair is controlled by viscous force below 1 kHz ( $R_A$  in Fig. 1) and the influence of the inertial force can be neglected [24]. This allows us to use the physical laws for a viscous fluid to calculate the maximal mechanical sensitivity which a hair can have.

Sensory hairs and antennae are sometimes highly feathered (Fig. 1). This leads to a large increase of the surface of the structure while only little increasing the mass, i.e., the viscous force can act more effectively on the structure.

### Sensitivity Limits for an Oscillation-Sensitive Hair

Ideal air-oscillation receptors should move exactly as the surrounding air, which could be true if the receptor had the same physical properties as the air. However, since sensory hairs have a 1 000-fold higher density than air this can never be achieved. If this receptor mass is, however, balanced by resistive and spring elements (Fig. 1) it is possible to get a hair that

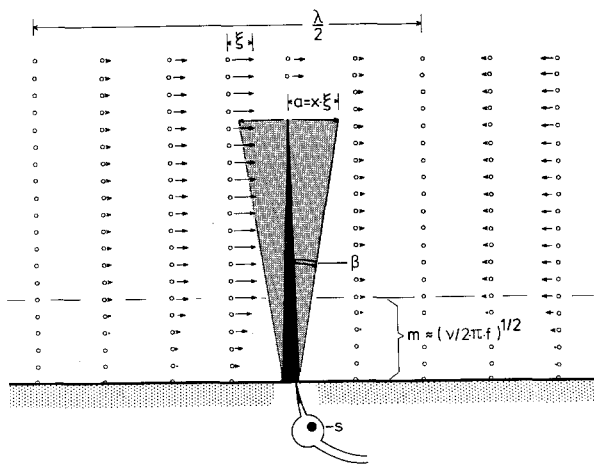


Fig. 2. Hair oscillation caused by particle (molecules of the medium) oscillation. For graphical demonstration of important parameters some idealized rows of molecules are shown. Arrows show direction and amplitude of displacement (propagation direction of the sound wave is perpendicular to the long axis of the hair).  $a$  Hairtip-displacement amplitude;  $f$  stimulus frequency;  $m$  thickness of boundary layer;  $s$  sensory cell;  $\beta$  deviation angle of the hair from resting position;  $\lambda$  wavelength;  $\nu$  kinematic viscosity;  $\xi$  particle-displacement amplitude;  $x$  factor see Eq. 5.

acts like an ideal receptor, although only in a limited frequency range because of the resonance characteristics of every mass/spring system [22]. Another complication arises from the fact that the hair is hinged at one end and thus goes through tilting movements, i.e., it cannot move exactly perpendicular to the wave front.

A purely theoretical treatment of hair motion in air [24] reaches conclusions that are in general agreement with previous experimental work results [22] although the theoretical model was developed under neglect of the inner friction ( $R_M$  in Fig. 1) of the hair articulation which may explain some discrepancies between the theoretical model and the experimental results. One important question in both investigations was: What is the theoretical limit for the mechanical sensitivity of a hair? It is obvious that a hair which for a given stimulus moves through a large amplitude is mechanically more sensitive than one which moves very little, provided the hair moves in both cases as a stiff rod. It is also evident that because of the mass/spring properties of the hair, the sensitivity threshold must be frequency-dependent. For judging mechanical sensitivity of a hair it is most useful to compare the amplitude of hairtip displacement with the amplitude of air-particle displacement at a given frequency rather than the deviation angle of the hair because the latter depends also on hair length. As derived in [24] a factor  $x$  gives the ratio of hairtip displacement to particle displacement in an

elastic medium at optimal mechanical sensitivity if the air-oscillation vector is perpendicular to the long axis of the hair:

$$x = \frac{3}{2} \left[ 1 + \left( \frac{\pi^2}{2(0.58 + \ln[1/2 \cdot R \cdot (2\pi f/\nu)^{1/2}])} \right)^2 \right]^{1/2} \quad (5)$$

( $R$  = radius of hair base,  $\nu = \eta/\rho$  kinematic viscosity). For  $10 \leq f \leq 400$  Hz  $x \approx 2$  in air which means that the hairtip moves with twice the oscillation amplitude of the air molecules. This optimum is reached in filiform hairs of caterpillars in the frequency range 100–400 Hz and for hair deviations not exceeding  $0.2^\circ$  from resting position [22].

### The Influence of Hair Length on Sensitivity

To reach the maximal hairtip-displacement amplitude possible under given stimulus conditions, the hair must exceed a minimum length  $m$ . The reason for this is that at the surface of an animal in a field of oscillating air the air particles are at rest. With increasing distance from the animal's surface the amplitude of the air oscillation increases until it reaches its final value at a distance  $m$  over the surface (Fig. 2). The thickness of this boundary layer can be given by

$$m \approx (\nu/2 \cdot \pi \cdot f)^{1/2}. \quad (6)$$

A mechanically optimally fitted hair should therefore be a few times longer than  $m$  [24].

On the other hand, the sensitivity of the whole sensory system depends not only on the mechanical properties of the sensory hair but also on those of the sensory cell, which means in this case that spikes are generated when a threshold hair deviation is reached. The best known threshold angle for impulse initiation for mechanoreceptive hairs is  $0.1^\circ$  [25]. With respect to the threshold angle of the sensory cell, very long hairs are obviously as disadvantageous as are very short ones for the mechanical reasons; the maximal possible deviation angle of the hair from resting position decreases at constant hairtip displacement (as defined by  $x$ ) with increasing hair length. Thus the threshold angle for impulse initiation may not be reached when the hair is very long. From these considerations a range of hair length of optimally adapted hairs can be estimated:

$2 \cdot m \leq \text{hair length} \leq 6 \cdot m$ . The limits of this range can float a little bit because there is no possibility for exact calculation; they must be estimated on the basis of the considerations above.

Since the thickness of the boundary layer  $m$  depends on frequency of air oscillation (Eq. 6) it is possible to

calculate in which frequency range a hair of given length is best adapted for receiving oscillation in the medium. This frequency range includes the mechanical resonance frequency of the hair. The experimental results on the hairs of caterpillars show that at small hair deviations ( $\leq 0.2^\circ$ ) the frequency range within which the hairs are optimally moveable is rather wide (100–400 Hz). At increasing hair deviation this frequency range is narrowed. At hair deviations  $> 0.4^\circ$  the hair moves well (but no longer optimally) only at its resonance frequency (100–150 Hz) [22]. (The fact that in trichobothria of *Tegenaria* no resonance frequency was found between a few Hz and 2 kHz [26] could result from shortcomings in the experimental method used, see p. 459.)

Figure 3 shows the calculated hair-deviation angles from resting position in a free-sound field at a constant stimulus intensity of 90 dB sound pressure (re.  $2 \cdot 10^{-5}$  Pa) at different stimulus frequencies and hair lengths. For this calculation it was assumed that the hairs are mechanically as sensitive as possible (see above). Values have been eliminated for which one or both of the following conditions is not fulfilled: 1)  $2 \cdot m \leq \text{hair length} \leq 6 \cdot m$ ; 2) deviation angle  $\geq 0.1^\circ$ . The remaining values relate hair length to their optimal frequency range. If the range of hair length will be extended over the range assumed here ( $2 \cdot m$  to  $6 \cdot m$ ) the frequency range to which a hair can respond will be extended, too. On the other hand, however, it will be restricted if the threshold angle of impulse initiation is bigger than  $0.1^\circ$  or if the mechanical sensitivity is not optimal. Since both are true for most described hairs in arthropods the relation between frequency range and hair length given in Figure 3 is most likely, although the uncertainty of correct hair-length range exists.

#### Anomalies in Published Sensitivity Thresholds of Air-Vibration-Sensitive Hairs

Experimentally the frequency range in which hairs sensitive to air vibration can be stimulated has been investigated in many cases. Table 1 gives the published values of this frequency range, the frequency  $f_{\max}$  of maximal sensitivity, and the sensitivity threshold at this frequency. The reported values of  $f_{\max}$  fit with the theoretically expected values as given in Fig. 3. However, many published sensitivity values are theoretically not possible and the hairs must be less sensitive in a free-sound field than the published data suggest. The following consideration prove this: Take a hair that is maximally moveable. The sensory cell has a threshold angle  $\alpha$  for impulse initiation in direction of maximal sensitivity. Then

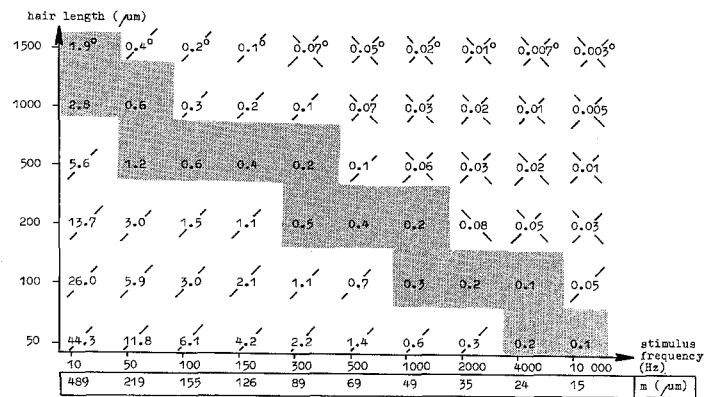


Fig. 3. Calculated maximum deviation angles from resting position for hairs oscillating in air at a constant stimulus intensity of 90 dB (re.  $2 \cdot 10^{-5}$  Pa) for different stimulus frequencies and hair lengths. It is assumed that the hairs are mechanically as sensitive as theoretically possible. 0.08: eliminated because the angle is smaller than the best known threshold angle of  $0.1^\circ$  [25]. 44.3: eliminated because hair length is not in the range  $2 \cdot m - 6 \cdot m$  ( $m$  thickness of boundary layer, see Eq. (6)). The remaining values (shaded area) show which hair length is suitable to receive which frequency

$$\tan \alpha = \frac{d}{l} \quad (7)$$

( $d$  = hairtip-displacement amplitude at threshold of impulse initiation,  $l$  = hair length,  $\alpha$  = threshold angle of impulse initiation, which is easily determined if the hair is fixed to the stimulus transducer).

As shown above in the case of maximal sensitivity we have

$$x \cdot \xi = d \quad (8)$$

( $x$  see Eq. (5)) which leads to

$$\xi = \frac{l \cdot \tan \alpha}{x} \quad (9)$$

If  $\xi$  is put in Eq. (3) one gets

$$p = \frac{l \cdot \tan \alpha}{x} \cdot \rho \cdot c \cdot 2 \cdot \pi \cdot f \quad (10)$$

If  $p$  is expressed in the usual dB scale it is

$$p[\text{dB}] = 20 \cdot \log \frac{l \cdot f \cdot \tan \alpha \cdot \rho \cdot c \cdot 2 \cdot \pi}{x \cdot p_0} \quad (11)$$

( $p_0 = 2 \cdot 10^{-5}$  Pa).

If all parameters are given in SI units one gets in air at  $15^\circ\text{C}$  and at sea level

$$p[\text{dB}] = 20 \cdot \log \frac{l \cdot f \cdot \tan \alpha}{x} \cdot 1.28 \cdot 10^8 \quad (12)$$

**Table 1.** Frequency range and sensitivity values that are published for different sensory hairs (discussion in text). All values were measured in electrophysiological experiments except the values published in [30] which were measured in behavioral experiments

Animal species	Location of hairs	Hair length [ $\mu\text{m}$ ]	Response-frequency range [Hz]	Best frequency $f_{\text{max}}$ [Hz]	Optimal threshold (re. $2 \cdot 10^{-5}$ Pa) [dB]	Ref.
<b>Orthoptera</b>						
<i>Chorthippus parallelus</i>	cerci		2 000–4 000		91	[78]
<i>Oxya japonica</i>	cerci		40–1 700	500	85	[79]
<i>Gryllus domesticus</i>	cerci		40–3 000	40	44	[80]
<i>Gryllus domesticus</i>	cerci	800–1 500	20–2 000	20	40	[81]
		150–800	20–2 000	80	53	
		< 150	300–1 500	800	88	
<i>Gryllus bimaculatus</i>	cerci	1 500–1 600	30–400	30	45	[27]
		600	30–700	30	50	
		< 600	30–2 000	30	62	
<i>Xenogryllus marmoratus</i>	cerci		30–2 000	800	65	[79]
<i>Homoeogryllus japonicus</i>	cerci		30–3 000	800	75	[79]
<i>Gryllotalpa hexadactyla</i>	cerci		100–600	200–600	77	[79]
<i>Acheta domesticus</i>	cerci		30–3 000	50–100	45	[82]
<i>Hentschoudentia epilamproides</i>	cerci		50–500	50	85	[83]
<b>Hymenoptera</b>						
<i>Apis mellifica</i>	head	640 $\pm$ 41	100–5 000	200–300	70	[8]
<b>Lepidoptera</b>						
<i>Heliconius</i>	head		400–5 000	1 200	61	[50]
<i>Barathra brassicae</i> (caterpillar)	thorax	508 $\pm$ 26	40–1 000	100–600	90 (100 Hz) –100 (600 Hz)	[30]
<i>Barathra brassicae</i> (caterpillar)	thorax	508 $\pm$ 26	40–1 000	150	91	[25]

Equation (11) gives the theoretical limit of sensitivity of a freely oscillating mechanoreceptive hair stimulated by particle vibration in a medium. If an experimentally determined threshold of sensitivity is below this maximal theoretically possible value (for air given by Eq. (12)), the measurements can clearly not be accepted as reliable. That several threshold values given in Table 1 are too low to be true is borne out by the following example:

Knjazev [27] found for 1 500  $\mu\text{m}$  long hairs in *Gryllus bimaculatus* at 30 Hz stimulus frequency a threshold of 45 dB. The only unknown factor here is the angle  $\alpha$  of threshold deviation of the sensory cell. If we assume  $\alpha = 1.0^\circ$ , the threshold intensity is at least 93.6 dB; if we assume  $\alpha$  to be  $0.1^\circ$ , the threshold intensity is at least 73.6 dB at 30 Hz stimulus frequency. If the mechanics of the hair are not optimal (which is true for *Gryllus bimaculatus* [28]) and/or the angle of impulse-initiation threshold is bigger than assumed, the thresholds would be even bigger than the calculated ones.

It is assumed that most investigators cited in Table 1 arrived at threshold values which were too low to be

possible because they neglected the influence of the near field of the stimulating sound source. If the preparation is brought nearer than  $\lambda/2$  to the sound source ( $\lambda/2$  for 30 Hz is about 570 cm in air) and the sound pressure is measured for calculating stimulus intensity, one gets only one component of the vectorially composed actual particle displacement (see p. 454). The dominant component of the hair-stimulating quantity, the near-field displacement, is neglected.

#### Sensitivity Characteristic of the Whole Sensory System

The sensitivity of sound receptors is traditionally defined by a frequency-dependent response curve, with intensity threshold being expressed in dB re.  $2 \cdot 10^{-5}$  Pa ("sound pressure-dB" = SP-dB). This is convenient for a sound-pressure-receiving system. However, since particle displacement at constant sound-pressure level decreases proportional to  $1/f$  (see Eq. (3)), threshold SP-dB values are of little use

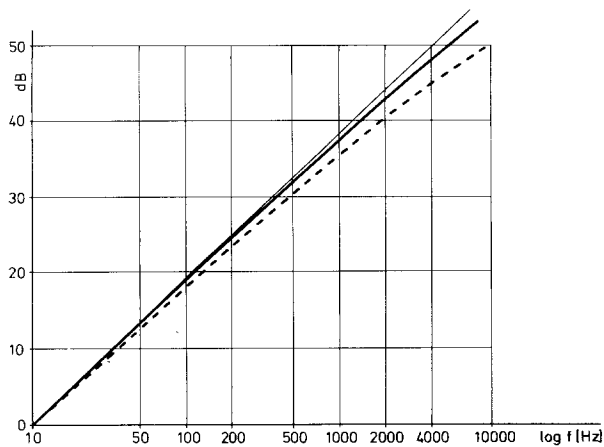


Fig. 4. Curves for calibration SP-dB threshold values (see text) for displacement-sensitive organs to make them comparable at different frequencies (for procedure of calibration see text). The absolute dB values given on the ordinate are arbitrary but this is irrelevant because the difference between the dB values of the compared frequencies is important and this difference can be taken directly from the ordinate. Thick solid line: hair oscillates in air; dotted line: hair oscillates in water; thin line: +6 dB/octave slope. The curves are calculated for a hair with a diameter of  $4\ \mu\text{m}$ , but the curves are rather independent on this parameter (see Eq. (5))

for comparing the sensitivities of medium-displacement receptors at different frequencies. However, it is possible to compare sensitivity values of sensory hairs expressed in the usual way (SP-dB, see above) if they are calibrated by using the curves given in Fig. 4. This calibration eliminates the difference in dB values that comes from pure mathematical treatment (see Eq. (3) and Eq. (5)). If the sensitivity curve (SP-dB) of a freely oscillating hair is determined and one wants to compare the dB values of two frequencies, the difference between the dB values of these two frequencies must be taken from the ordinate of Fig. 4 and this difference must be subtracted from the experimentally found SP-dB of the higher of the two compared stimulation frequencies. The raise of the calibration curves in Fig. 4 is not exactly +6 dB/octave as would result from Eq. (3). They must be raised less, because the factor  $x$  (that gives the maximal mechanical sensitivity value) increases slightly with frequency (see Eq. (5)).

The diagram given in Fig. 4 can also be used for underwater sound. In underwater acoustics the reference for sound pressure is commonly  $1\ \text{dyne}/\text{cm}^2$ , which lies +74 dB above the reference in air ( $2 \cdot 10^{-4}\ \text{dyne}/\text{cm}^2$ ) which must be considered if the sensitivity values among these two media are compared.

## Methods and Problems in the Experimental Analysis of Mechanical Properties of Sensory Hairs

The standard procedure for testing whether an animal is sensitive to sound pressure or to medium-particle oscillation is to place it in the sound field of a standing wave where pressure- and medium-oscillation maxima are separated by  $\lambda/4$  in space [29, 30]. Such a standing wave results if the sound wave emitted by a loudspeaker is reflected by a stiff wall so that the emitted and the reflected waves interfere with one another resulting in maximal amplitudes of pressure and displacement that are twice that of the emitted wave (Kundt's tube, Fig. 5a). The condition for an optimal standing wave is a defined frequency-dependent distance between loudspeaker and reflecting wall. A standing wave results also inside a closed air-filled box that is moved sinusoidally around its resting position (Fig. 5b). The sound-pressure and particle-oscillation functions inside the box are for a first approximation those that are found at the pressure node and displacement loop in a standing wave shown in Fig. 5a. When using this vibrating box one has to consider the dimensions of the box, i.e., the inner diameter of the box in direction of vibration should not be too large. Otherwise the value of particle displacement calculated from measured acceleration of the box (Fig. 5b) cannot be trusted (for detailed formulae see [22]). Under the precisely defined conditions of a standing wave many mechanical properties of the sensory hairs can be investigated since it is not necessary to measure the air-particle displacement directly; it can be calculated from the easily measurable sound pressure (Fig. 5a) or acceleration (Fig. 5b). Air-particle movement can also be calculated from the measured sound pressure if the preparation is placed in the far field of a sound source (Fig. 5c) but here it is very difficult to exclude unwanted air disturbances, e.g., those caused by the experimenter. Stronger air oscillations can be measured directly by a calibrated hot-wire anemometer. The calibration can be done by using one of the methods shown in Fig. 5 if the anemometer is substituted for the preparation.

One must be careful in using other sources of force than air oscillation to deflect medium-vibration-sensitive hairs. Most of these hairs are electrostatically moveable, but it can be shown by a simple experiment that using electrostatic force to bring a hair to oscillation is not a suitable method for determining the mechanical frequency response, e.g., the resonance frequency of the hair with its associated air load. To show this, a hair of *Barathra* caterpillars was first stimulated by air oscillation and the stimulus intensity set so that a definite oscillation amplitude of the hair was reached. Then the hair was stimulated by an AC voltage of another frequency and brought electrostatically to the same amplitude of hair deviation (method of electrostatic stimulation see [26]). Then the

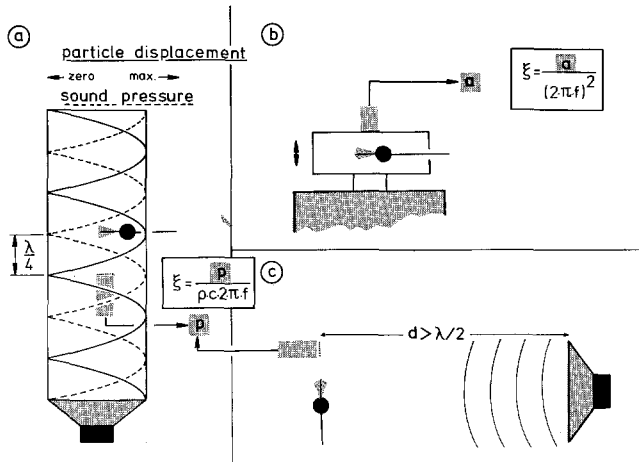


Fig. 5. Methods for determination of particle displacement that stimulates a sensory hair. (a) Kundt's tube, (b) vibrating box, (c) open sound field. *a* Acceleration (peak value); *c* sound-propagation velocity; *d* distance to the sound source; *f* stimulus frequency; *p* sound pressure (peak value); *λ* wave length; *ξ* particle-displacement amplitude; *ρ* density of the medium

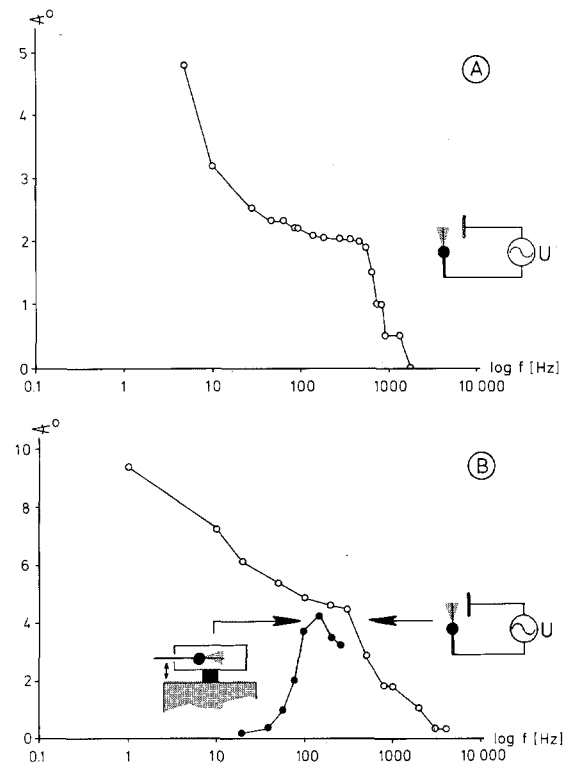


Fig. 6. Demonstration of the outcome using different methods of investigation of the mechanical properties of a sensory hair. (A) Response curve (deviation angle of the hair vs. stimulation frequency) resulting from the use of electrostatic hair displacement for trichobothria of *Tegenaria* spiders (curve after [26]). Measurements were done in vacuum at a constant AC voltage of unknown value, that exceeded 40 V. (B) Open circles show the result of the same experiment described for (A) for a filiform hair of a *Barathra* caterpillar. Measurements were done in air at a constant AC voltage of 60 V (peak-peak). Filled circles show the results from stimulating the same hair by air vibration with a constant velocity of the air particles. It is evident that the resonance at 150 Hz of the hair in the oscillating medium is completely suppressed if the hair is driven to forced oscillation by AC electrostatic force

hair was simultaneously stimulated by the air oscillation and the electrostatic force of another stimulus frequency. The result was that the air oscillation had absolutely no influence on frequency and amplitude of the hair oscillation. The hair oscillates always with the frequency of the AC voltage. This was found to be true for all frequencies used (10–1 000 Hz), independent whether the AC-voltage frequency was higher or lower than the air oscillation, and independent of the frequency difference between the two forces. This shows that the electrostatic force is so strong that the resonance properties of the hairs are masked, i.e., the electrostatic force acts as if it were tightly coupled to the hair. One can assume that this happened in the experiments on trichobothria of *Tegenaria* spiders, where no resonance point could be found in fresh preparations by using the electrostatic method of hair deviation [26]. Figure 6 demonstrates the complete disagreement between experimental results depending on whether the inadequate method of electrostatic hair stimulation or the physiological stimulation of the hair by medium vibration is used.

### Biological Function of Medium-Oscillation Reception

Medium-vibration-sensitive receptors can be used for detecting enemies, for localizing prey, or for communication.

The ability to detect a source of mechanical disturbance in a medium is found throughout the animal kingdom from Protozoa to Vertebrata. Positive vibrotaxis is described e.g. for *Amoeba proteus* where a stimulation frequency of 50 Hz is most effective [31]. Prey localizing by non-motile cilia by means of small displacements in the surrounding water has been described for Ctenophora [32]. The marine gastropod *Patella* reacts with avoidance and flight behavior if stimulated by water displacements. The receptors are not known in this case [33]. Chaetognatha grasp for source of periodical water displacement preferably of 10–14 Hz. This behavior is triggered by stiff cilia and bristles widespread on the epidermis [34]. Their main prey are copepods which produce water displacement of 10–20 Hz during filter feeding and swimming [35].

The spiders *Agelena labyrinthica* and *Sericopelma rubronitens* turn and often grasp precisely for an object vibrating in air, e.g., a whirring fly, even when they are blinded. After destruction of the trichobothria this capacity is abolished [36, 37]. Thus, trichobothria may play an important role in localizing prey, especially under poor-light conditions (in dark corners; at night).

Water-displacement receptors are widespread among Crustacea. Sensory hairs that respond to water oscillation have been described several times [38–42]. A chordotonal organ in the antennae can also receive water displacements which are transmitted as flagellar movements [43, 44]. It is assumed that this sensory capacity helps the crustaceans to detect predatory fishes.



The biological function of medium-oscillation reception in insects is better known. The caterpillars of *Barathra brassicae* detect the air vibrations generated by the wingbeat of approaching predators (wasps) or parasites (wasps, flies), and show defensive reactions that raise their chance of survival by about 30% [5]. The sensory hairs responsible for the reception of the air oscillation are optimally adapted to receive this natural stimulus [22, 25]. Defensive reactions on stimulation by the flight sounds of parasitic insects have also been described for tent caterpillars [45]. Escape reactions are also released by stimulation of the cercal filiform hairs in different Orthoptera [46]. In cockroaches wind produced by the tongue strike of a toad elicits escape behavior [47].

A function of cercal filiform hairs in intraspecific communication might be possible in the African cricket *Phaeophilacris spectrum*. During mating and aggression the male flicks its wings and by this produces an air vibration directed towards the female or a competitor [48].

Self-stimulation of the filiform hairs on the cerci of cockroaches by their own wingbeat may also be important for flight stabilization [49]. A similar function is assumed for the sensory hairs that compose the Jordan's organ on the head of some butterfly species [50]. The antennae oscillations forced by the own wingbeat help measuring and regulating diverse flight parameters in *Calliphora* [51–54]. Displacement sensitivity of the Johnston organs has been demonstrated for much more flies and mosquitos [55–62]. The ability of Diptera to receive air-particle displacement is most important in courtship. The males of *Aedes* and *Anopheles* are attracted by a sound in the frequency range 300–400 Hz with a best frequency of about 400 Hz. The wingbeat of the females lies in the range 350–400 Hz, i.e., around the resonance frequency of the male antennae. The wingbeat of the male is in the range 500–550 Hz and thus releases no behavioral response in other males. In *Drosophila* the males produce air displacements by vibrating one wing in a species-specific pattern [63] that is received by the females through their antennae [64, 65].

Dragonfly larvae detect prey by receptors on the antennae and on the tarsi that are stimulated by water displacement [66]. The same is observed for *Ranatra linearis* where sensory hairs on the forelegs must be stimulated [67].

In vertebrates the best known receptor system for particle displacement in water is the lateral line organ in fishes and amphibians [68]. This organ is used for spatial orientation or for localizing moving prey [69–73]. In addition the lateral line system plays an important role in schooling behavior of fishes [74].

The lateral line organ is also involved in agonistic behavior where strong water displacements are produced by tail flicks of parallel or antiparallel displaying fishes. It has been assumed that the strength of the competitor in this ritualized fight is estimated from the strength of stimulation of the lateral line organ [75].

A problem in structures being very sensitive for particle displacement is self-stimulation while the animal moves actively around. One mechanism for solving this problem is the decrease of the sensitivity of interneurons involved in the control of reactions to displacement stimulation while the animal is walking, which has been found in *Periplaneta* [76] and in the crustacean *Petrochirus californiensis* [77].

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