Acoustical Response of Hair Receptors in Insects

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Summary. A detailed mechanical model is developed to account for the behaviour of hair-like acoustical sensory receptors in insects. For the small hair diameters commonly found, it is concluded that the force acting on the moving hair is caused almost entirely by the viscosity of the air, as analyzed long ago by Stokes. The result of this viscous force is to provide a bending moment about the base of the hair that is proportional to the acoustic particle velocity but that lags behind it by about 135°. In addition the viscous force increases the moment of inertia of the hair by a large and frequency dependent addition, and provides a viscous damping term of sufficient magnitude to reduce the Q value to near unity.

The measurements of Tautz (1977) on the thoracic hairs of the caterpillar *Barathra brassicae* are discussed in detail in terms of the model. Many of these observations are well accounted for, though a few discrepancies remain.

Introduction

In a recent paper Tautz (1977) has reported careful and detailed measurements on the mechanical response of sensory hairs in the caterpillar of *Barathra brassicae* over the frequency range 10–1000 Hz. The hairs studied were divided into two classes: straight hairs which showed uniform deflection sensitivity for sound waves incident from any direction in the plane perpendicular to their length, and bent hairs which showed maximal sensitivity for sound incident from a direction normal to their plane.

For both types of hairs behaviour was essentially linear up to angular displacements of about 10°, above which angle the hair became stiffer. The straight hairs when excited with an acoustic signal having constant acceleration amplitude, showed a peak sensitivity near 100 Hz, at which frequency the hair tip displacement amplitude was nearly equal to twice the acoustic displacement amplitude of the sound wave for small displacements but somewhat less than this for large amplitudes. The bent hairs showed similar, though rather smaller, sensitivity when excited in their orientation of maximal response. The sensitivity was rather less than half this value for excitation from a direction at 90° to the direction of maximum sensitivity.

When sensitivity was assessed in terms of acoustic particle displacement necessary to achieve a given hair tip displacement, it was found that sensitivity increased at about 6 dB/octave below the sensitivity peak near 100 Hz and decreased at −12 dB/octave above this peak (Tautz, 1977, Fig. 7). At very small displacement amplitudes (1 μm) the sensitivity showed a plateau region between 100 and 400 Hz but it is not clear to what extent this is accounted for by the limited resolution of the tip motion measurement.

It should be noted, however, that these sensitivity measurements are somewhat at variance with those presented in Tautz's Figure 5 which show a rise in sensitivity of 12 dB/octave below 100 Hz and a fall of −6 dB/octave between 100 and 250 Hz for excitation at constant acoustic acceleration amplitude. Converting this to constant acoustic displacement amplitude, we should expect a rise of 24 dB/octave below 100 Hz and a continuing rise of 6 dB/octave between 100 and 250 Hz. This is very different from the data presented in his Figure 7. The amplitudes of displacement in Figure 5 are, however, many times greater than those of Figure 7, and both figures show a good deal of non-linearity in behaviour (i.e. an increase in stimulus level does not simply produce a scaled-up version of the original response curve). These uncertainties mean, however, that we should perhaps have some reservations about this particular aspect of the measurements.

Stroboscopic observation of the relative phase of the hair motion and that of the air, defined by the motion of a surrounding box, established that, near 100 Hz, the motion of the hair lagged behind that of the medium by about 90°, though the expression is a trifle ambiguous and the motion of the hair may in fact be in advance of that of the medium by this amount.

Finally, by releasing the hairs from a displaced position and observing the resulting motion, Tautz concluded that each hair behaves as a highly damped simple harmonic oscillator with a damped period of about 8 ms and a quality factor Q of about unity. This suggests a true resonance frequency of about 150 Hz (see Morse, 1948, p. 24).

In view of the availability of these observations, and because Tautz attempted only an elementary analysis of the physical behaviour involved, it seems worthwhile to carry these discussions a stage further and to present a more careful treatment of the behaviour of a hair in a sound field.

Accoustical Fundamentals

The action of a sound wave on a cylinder is discussed in standard texts on acoustics (e.g. Morse, 1948) in an approximation which neglects the viscosity of the air. For the case in which the cylinder radius r is much less than the sound wavelength λ, then the force on unit length of the cylinder can be shown to have amplitude

$$F = 8\pi^3 (r^2/\lambda) p \tag{1}$$

when the sound pressure amplitude is p. For the insect hairs in our present problem $r \approx 2 \,\mu m$ and $\lambda \approx 3$ m so that F is completely negligible.

The reason for this is that the force arises from the difference in the pressure acting on the front and back surfaces of the cylinder, and when $r \ll \lambda$ this difference is very small. The same situation occurs in sound radiation from vibrating strings, which are so inefficient in this respect that stringed musical instruments must always be provided with a soundboard which is set in motion by the string vibrations and then radiates them to the air as sound.

The second way in which a cylinder can interact with a fluid, with respect to which it is in motion, is through viscous forces. The problem of direct interest to us here does not appear to have been treated explicitly but the inverse problem of the damping of a vibrating cylinder by fluid viscosity was treated long ago by Stokes (1851). The two problems are essentially equivalent, provided that the cylinder radius r is much smaller than the sound wavelength involved,

a condition which is certainly satisfied in our present situation.

In Stokes' treatment, he separates the force per unit length on the hair into two components which are 90° out of phase with each other. The component F_1 in phase (or rather 180° out of phase) with the cylinder velocity acts as a damping force, while the component 90° out of phase appears as a mass added to that of the cylinder itself. Physically the first force component is contributed by the fluid that streams past the cylinder while the second arises from the fluid carried along with it.

Because the hairs in our present problem are of very small radius r and the frequency f is very low, the parameter

$$s = \tfrac{1}{2} r (2\pi f/v)^{1/2} \tag{2}$$

used by Stokes, where v is the kinematic viscosity of the fluid, is very small and we can use the result appropriate in the limit $s \ll 1$. For an infinite cylinder of radius r vibrating at frequency f and with velocity $v = v_0 \cos 2\pi ft$, the damping force F_1 per unit length is given by

$$F_1 = 2\rho v G v \approx 2\rho v G v_0 \cos 2\pi ft \tag{3}$$

where

$$G = -g/[g^2 + (\pi/4)^2] \tag{4}$$

$$g = 0.58 + \ln s \tag{5}$$

and ρ is the density of the fluid. The force acting in antiphase with the acceleration of the cylinder, which appears in Stokes' case as an added mass, can be written as

$$F_2 = (-\pi v \rho G/2gf)\, \dot{v} \approx (\pi^2 v \rho G/g)\, v_0 \sin 2\pi ft. \tag{6}$$

From the form of (2), (4) and (5) it is clear that g, and hence G, F_1 and F_2, depend only weakly on cylinder radius r and frequency f.

For later reference we note the numerical values $\rho = 1.2 \,\mathrm{kg \cdot m^{-3}}$ and $v \approx 1.5 \cdot 10^{-5}\,\mathrm{m^2\,s^{-1}}$ for air under ordinary conditions. For our present biological problem $r \approx 1-2 \,\mu m$ and $f \sim 100$ Hz which implies $s \approx 0.003 - 0.006$, $g \approx -5$ and $G \approx 0.2$. The added mass implied by (6) is equivalent to the mass of a hair of radius about 2 μm, so that the correction involved is very considerable.

Hair Receptor Model

The straight hair receptors described by Tautz (1977) have the form of elongated cones about 500 μm in length and 2.5 μm in basal radius. Stroboscopic ob-
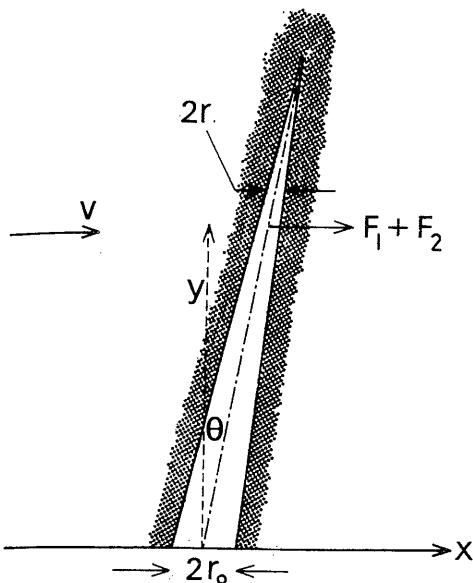
Fig. 1. Dimensions and coordinates for the hair detector model. Shading shows the co-moving air mass

servation shows that they deflect rigidly about their bases without bending. We therefore now construct a careful model for this behaviour, assuming the sound wave to be incident from a direction perpendicular to the axis of the hair.

Let y be the coordinate measured along the hair axis from its base and r_0 the basal radius of the hair as shown in Figure 1. Then the radius at distance y from the base is

$$r=r_0(1-y/l) \tag{7}$$

where l is the length of the hair. Since the problem is one of angular deflection about a fixed point at the base of the hair, we need to calculate the moment of inertia I_h of the hair about an axis through this point and perpendicular to the hair axis. This is given by

$$I_h=\int_0^l \pi\rho_0 r^2 y^2\, dy=\pi\rho_0 r_0^2 l^3/30 \tag{8}$$

where ρ_0 is the density of the material of the hair ($\rho_0\approx 1100\ \mathrm{kg\ m^{-3}}$).

Because in our problem both the hair and the surrounding medium are moving, we cannot simply add the extra mass and moment of inertia implied by (6), as can be done for a hair executing a damped motion in stationary fluid. Rather, we must examine the motion more carefully.

Suppose that at some instant the deflection of the hair is $\theta=\theta_0\sin(2\pi ft-\delta)$, then the velocity of motion of an element of hair at a distance y from the base is $\dot{x}=y\dot{\theta}$ and the velocity of the neighbouring air relative to this element, which must replace v in (3)

and (6) is $v-\dot{x}$, where v is the instantaneous particle velocity in the sound wave. Since both v and $\dot{x}$ vary sinusoidally with frequency f, we can therefore use (3) and (6) to find the forces $F_i(y)$ on an element of hair of unit length at distance y

$$F_1(y)=2\rho v(v-y\dot\theta)\, G, \tag{9}$$

$$F_2(y)=(-\pi\rho vG/2gf)(\dot v-y\dot\theta). \tag{10}$$

Now, as we have seen, G and g vary little with r and are hence nearly constant along the length of the conical hair. The moments of these two acoustic forces about the base of the hair are therefore

$$L_1=\int_0^l F_1 y\, dy\approx \rho vGl^2(v-2l\dot\theta/3) \tag{11}$$

$$L_2=\int_0^l F_2 y\, dy\approx(-\pi\rho vGl^2/4gf)(\dot v-2l\dot\theta/3). \tag{12}$$

This discussion clearly begs the question whether or not Stokes' treatment, derived for infinitely long cylinders, can be applied directly to cylinders of finite length. We conclude later that, with certain reservations, such an extension is valid in the present case.

Since the hair is anchored more or less elastically at its base, it has exerted on it a restoring torque $k\theta$ when it is deflected through an angle θ. This restoring torque, which is presumably the quantity affecting the neural transducer cells, will generally contribute also some viscous losses, but we can ignore these in comparison with the damping effect of the air acting on the hair itself. The equation of motion of the hair is thus

$$I_h\ddot\theta+k\theta=L_1+L_2 \tag{13}$$

which, by (11) and (12), can be written as

$$(I_h+I_a)\ddot\theta+\tfrac{2}{3}\rho vGl^3\dot\theta+k\theta=\rho vGl^2\left(v-\frac{\pi\dot v}{4gf}\right) \tag{14}$$

where

$$I_a=-\pi\rho vGl^3/6gf \tag{15}$$

is the moment of inertia contributed by the air carried along with the hair, and for convenience we can write $I=I_h+I_a$. Since I_a is positive and varies as $1/f$, it represents an increasingly important contribution at low frequencies. For the hairs of caterpillars of *B. brassicae* $I_a>I_h$ for $f<f_1\approx500$ Hz and, near the resonance frequency $f_0\approx150$ Hz, I_a is about $3I_h$.

Since $v=v_0\cos 2\pi ft$, we can write, in the right side of (14),

$$v-\pi\dot v/4gf=v_0[1-(\pi^2/2g)^2]^{1/2}\cos(2\pi ft-\delta_0) \tag{16}$$

where

$$\delta_0 = \tan^{-1}(\pi^2/2g) \tag{17}$$

so that the forcing term in (14) lags behind the air velocity v by the angle δ_0. Since $g \approx -5$ in the present case, $\delta_0 \approx -45°$.

Using (16) in (14) we see that this equation represents the behaviour of a damped simple harmonic oscillator excited by a sinusoidal force of frequency f. The resonance frequency f_0 is given by

$$f_0 = (1/2\pi)(k/I)^{1/2} \tag{18}$$

which serves to determine k if f_0 and I are known.

If $f = f_0$ then $I\ddot{\theta} + k\theta = 0$ in (14) so that it becomes

$$I\ddot{\theta} = \tfrac{3}{2}[1 + (\pi^2/2g)^2]^{1/2} v_0 \cos(2\pi f_0 t - \delta_0). \tag{19}$$

Integrating to find the displacement $d = l\theta$ of the hair tip, we find

$$d = \tfrac{3}{2}[1 + (\pi^2/2g)^2]^{1/2} a_0 \sin(2\pi f_0 t - \delta_0) \tag{20}$$

where $a_0 = v_0/2\pi f_0$ is the amplitude of the air displacement. Since $g \approx -5$, (20) shows that, at this resonance, the amplitude of the tip displacement is very closely twice the amplitude of the air displacement. The hair displacement is in advance of the air displacement in phase by an amount $-\delta_0$ which, as we have seen, is about 45°.

The resonance frequency f_0 is the frequency of maximum response when the acoustic velocity amplitude is maintained constant. From Tautz's measurements this frequency is about 150 Hz for $B.\ brassicae$. From (14) the Q-value at the resonance is given by

$$Q = 3\pi f_0 I/\rho v G l^3 \tag{21}$$

the formal definition of Q being given by Morse (1948, p. 25). Substituting values appropriate to the present problem we find $Q \approx 1$, which is closely the conclusion reached experimentally by Tautz.

It is interesting to note that, for the sensory hairs of $B.\ brassicae$ near the resonance frequency, both the inertia and the damping of the hair are determined primarily by the air medium rather than by the dimensions or other properties of the hair itself. Only the elastic restoring force on the hair base is important because of its role in determining the resonance frequency.

It is possible, however, that details of the elastic and viscous properties of the base mounting of the hair may become important under more extreme conditions. This base support is almost certainly responsible for the non-linearity observed by Tautz at large displacement amplitudes and it may also con-

tribute to deviations from the expected behaviour at high frequencies, which we discuss below.

Frequency Response and Phase Shift

The frequency response of our model is completely defined by (14) and is most usefully considered in three ranges $-f < f_0$, where f_0 is the resonance frequency defined by (16), $f_0 < f < f_1$, where f_1 is the frequency at which the moment of inertia of the hair itself exceeds that of the air load, as defined by (8) and (15), and finally the region $f > f_1$. We note that in the present case $f_0 \approx 150$ Hz and $f_1 \approx 500$ Hz.

For $f < f_0$, the term $k\theta$ dominates the left side of (14) and we find that $\theta \propto v$ or equivalently $\theta \propto af$, where a is the acoustic displacement amplitude in the sound wave. If a is constant then the hair tip displacement $d = l\theta$ rises with increasing frequency at 6 dB/octave.

For $f_0 < f < f_1$, the term $I\ddot{\theta}$ dominates the left side of (14) and, by (15), $I \propto f^{-1}$ so that $d \propto f^0$ and the hair-tip displacement is independent of frequency.

For $f > f_1$ again $I\ddot{\theta}$ is dominant, but now I is independent of f, so that $d \propto f^{-1}$ and the response at constant acoustic displacement amplitude should fall at -6 dB/octave with increasing frequency. Of course, the transitions between these three domains are not sharp.

We have already remarked on the uncertainty in the interpretation of some of Tautz's sensitivity data and it is perhaps sufficient to note that our predictions roughly confirm the results presented in his Figure 7, except that his measured decrease in sensitivity above 500 Hz is about -12 dB/octave rather than our predicted -6 dB/octave. The predicted plateau region between 150 and 500 Hz is present on his low-amplitude curves but it acquires a slope of about -3 dB/octave and decreases in frequency range at higher amplitudes.

Finally, we note Tautz's observation that at 100 Hz the motion of the hair differed from that of the medium by 90°. Now (Morse, 1948) for an oscillator with resonant frequency f_0 and quality factor Q, the phase lag of velocity behind force, and thus in the present case of hair velocity behind the forcing term (16) is

$$\delta_1 = \tan^{-1}[Q(1 - f_0^2/f^2)]. \tag{22}$$

If $f_0 \approx 150$ and $f = 100$ Hz, as in Tautz's measurement, and $Q \approx 1$, then $\delta_1 \approx -50°$, so that the velocity of the hair tip is about 50° in advance of the forcing term. Since from (20) this forcing term is itself in advance of the acoustic velocity by $-\delta_0 \approx 45°$, the

hair velocity should be in advance of the air velocity, and thus the hair displacement in advance of the air displacement, by $-(\delta_1+\delta_0)\approx95°$. This conclusion is only partly in agreement with the measurements of Tautz who observed a phase shift of 90° at this frequency but stated that the hair motion was retarded rather than advanced in phase by this amount. The definite nature of our theoretical conclusion suggests that the observation should be re-checked specifically on this point. Tautz (personal communication) has suggested that the discrepancy may perhaps be caused, at least in part, by non-uniform motion of the air within his measurement box.

Adjustments to various parameters have to be made if the hair radius is greatly different from 1 μm or the frequency greatly different from 100 Hz, but with this reservation the hair displacement should lead the air displacement by about 135° at frequencies well below f_0 and lag by about 45° at frequencies well above f_0.

Conclusions

We have produced a first-order linear model for the behaviour of a receptor hair in a sound field which goes some way towards explaining the available observations on B. brassicae. The model is, of course, of quite general applicability to receptor hairs on any animal.

The model is deficient in several respects. In the first place it is linear, while for large hair-tip displacements the air flow and hence the behaviour is almost certain to have appreciable non-linearity. In the second place we have used Stokes' treatment which was derived for cylinders of infinite length, and applied it to quite a short cylinder. This procedure is reasonable provided the end effects do not extend far along the hair. A criterion for this is that vorticity diffuse a distance small compared with the hair length in a time $2\pi f$. This requires that

$$l>(v/2\pi f)^{1/2} \tag{23}$$

where v is the kinematic viscosity of air. For the present case this sets the lower limit of frequency for which the analysis is roughly valid at about 10 Hz.

There is one other physical feature of the problem that was ignored in the formulation of our simple mechanical model. This is the existence of a viscous boundary layer at the surface on which the hair is mounted. Clearly the air at the surface is stationary and the acoustic displacement reaches its full amplitude only at some distance y_0 above the surface. At frequency f the thickness of this boundary layer is roughly

$$y_0\approx(v/2\pi f)^{1/2} \tag{24}$$

thus, at a frequency of 150 Hz, $y_0\approx100$ μm. Clearly for good response the hair receptor must have a length l substantially greater than y_0. This is nicely satisfied for B. brassicae in which $l\approx500$ μm. In fact a hair much longer than this would show a decrease in sensitivity since, as we have seen, the hair-tip displacement at resonance is closely twice the acoustic displacement so that the angular displacement at the base, which is presumably the quantity transduced neurally, is inversely proportional to hair length for l much greater than y_0. A hair length equal to a few times y_0 is therefore optimal.

This analysis leads us to expect that hair-like transducers should have a length roughly in inverse proportion to the square root of the frequency they are designed to detect. The radius of the hair is important only in so far as it enables the hair to remain stiff. The structure of the base mounting should be such as to ensure an elastic restoring force sufficient to give a resonance frequency for the hair and its associated air load that is close to the frequency to be detected.

Comparison of the conclusions drawn from our model with Tautz's measurements on B. brassicae shows good agreement in many features but some obvious discrepancies. It is not yet clear whether these discrepancies are caused by shortcomings in the theory or by uncertainties in the measurements or in their interpretation.

References

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