Mechanical polarization in the air-current sensory hair of a cricket [1]

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Summary. We examined the mechanical anisotropy of the basement spring which underlies the directional sensitivity of the cercal filiform hair of the cricket (*Gryllus bimaculatus*). Spring stiffness varied with the direction of hair deflection. The anisotropic ratios were 8 for short hairs and 4 for long ones, whereas the absolute values of spring stiffness varied 100-fold with hair length.

Key words. Cricket; air-current sense; filiform hair; directional mobility; spring stiffness.

Crickets and cockroaches detect air fluctuations caused by the motions of predator toads or parasitic wasps [4]. They respond with either escape running, a defensive posture or kicking [5-7]. The viscous force from the air flow deflects filiform hairs on the cerci, the rear end appendages of orthopteran insects. Mechanoreceptor cells of the hairs transmit signals indicating the velocity, acceleration and direction of air flow to the central nervous system [8,9]. Cockroaches utilize the sensory signal of wind acceleration as a cue for an escape decision [11].

The filiform hair sensory system of crickets detects the velocity and acceleration of air flow quite separately. The long filiform hairs are sensitive to velocity, and the short ones to acceleration [10]. The air close to the surface of a body tends to stagnate on it, i.e. shows increased viscosity. The boundary layer in which the velocity of flow changes with the distance from the surface becomes thinner when the flow has a higher acceleration. As a result, the way in which a filiform hair acts as a mechanical filter depends on its length [12]. During post-embryonic development, the mechanical properties of the hair structures are adjusted so as to keep the receptor function unchanged throughout the ecdyses [13].

Directional sensitivity is essential if a cricket is to localize the source of air fluctuation, and three types of cricket cercal filiform hairs with different directions of best mobility to air fluctuation have been classified [14,15]. They are the L-, T- and D-hairs, whose directions of best mobility are the longitudinal, transverse and diagonal axes of the cercus, respectively. Only a few studies have examined the mechanical properties which underlie directional mobility of the filiform hairs [15,16]. In this paper, we describe the mechanical anisotropy of the hair-supporting spring as a basis of directional sensitivity.

Spring stiffness was measured as follows. A dissected cercus was mounted on the stage of a horizontal microscope. The orientation of the plane of best mobility of a hair was confirmed by applying air puffs. A small sphere of polymethylmethacrylate (20–80 μm in diameter, mass density 1.2×10^3 kg/m^3) was loaded on the hair shaft as a known weight. The whole microscope was then rotated into an upside-down position and we measured the angular displacement of the hair shaft by the force of gravity acting in the opposite direction. Spring stiffness is given by the ratio of hair deflection to the torque due to the force of gravity acting on the weight. Details of the measurement have been described previously [12].

The results are shown in the figure. Except for the cases marked 'New' in the figure, the data come from adult crickets 1–2 weeks after imaginal molt. The spring stiffness of the L-hairs when deflected parallel to the longitudinal axis of the cercus (L-L in the figure) fits well with our previous measurements [12,13]. The spring stiffness increases in proportion to the square power of hair length. The T-hairs' spring stiffness when deflected in the direction of the transverse axis of the cercus (T-T in the figure) was similar to the L-L stiffness.

When the hairs were deflected perpendicularly to the plane of best mobility (T-L and L-T in the figure) the
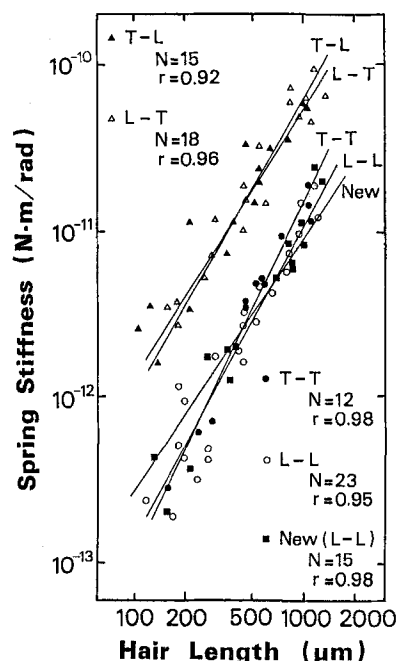
Stiffness of hair-supporting springs (ordinate) are plotted in relation to the hair length (abscissa). Both scales are logarithmic. Five different cases are plotted with different symbols. T-L shows the results of the spring stiffness measurement of T-hairs deflected in the L-direction (parallel to the longitudinal axis of a cercus). In the same manner, L-T shows the result of subjecting L-hairs to T (transverse) deflection, L-L shows the response of L-hairs to L-direction and T-T shows that of T-hairs to T-direction. New (L-L) refers to insects within 1 h after imaginal ecdysis.

springs showed much greater stiffness. In the cases of both the L- and T-hairs, the stiffness in this plane was about 4 times greater in the long hairs and about 8 times greater in the short ones than in the plane of best mobility. Except for the orientation of the plane of best mobility, L- and T-hairs have the same mechanical properties: these include the length-stiffness relation and the spring anisotropy. The orientation of the plane of best mobility depends upon positional information at the time of differentiation from an epidermal mother cell[17]. The information is translated into the alignment of the tormogen cell which secretes the anisotropic spring diaphragm.

The amount of L-L stiffnesses measured in the filiform hairs of crickets within 1 h after imaginal ecdysis ('New' in the figure) showed no difference when compared with the results for older animals. The springs seem to be functional from the time just after ecdysis. No further tanning seems to be necessary to establish the mechanical sensitivity of the cercal filiform hairs, whereas the body wall cuticle must be tanned for a couple of hours to achieve full strength.

The thoracal filiform hairs of *Barathra* caterpillars regain their maximal sensitivity within a few minutes of ecdysis[18]. During ecdysis, when the cuticular structures of hair sensilla are replaced, the hairs suffer a loss of sensitivity to air-motion. It is crucial for all cuticular mechanoreceptors that this blind period should be as short as possible. Although the recovery of sensitivity after ecdyses has not yet been studied in the cercal sensory afferents, we have at least found that the mechanical parts are functional just after ecdysis.

The directionality of hair mobility under an oscillating air current shows a figure of eight[15]. The ratio between amplitudes with respect to the plane of best mobility and those which are perpendicular to it agree well with the polarization of spring stiffness which we have found here. The directional mobility of cricket sensilla in response to air fluctuation is a direct reflection of the polarizing spring.

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Functional similarities in the mechanical design of the aorta in lower vertebrates and mammals

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Summary. The mechanical properties of the aorta from the toad *Bufo marinus*, the lizard *Gekko gecko* and the garter snake *Thamnophis radix* were compared to those of the rat, by inflation of vessel segments in vitro. The arteries of the lower vertebrates, like those of mammals, were compliant, higly resilient, and non-linearly elastic. The elastic modulus of the artery wall was similar in the lower vertebrates and mammals, at their respective mean physiological pressures. We conclude that the aorta in each of these animals is suitably designed to function effectively as an elastic pulse smoothing component in the circulation; differences in the pressure wave transmission characteristics of lower vertebrates and mammals do not result from dissimilarities in arterial elastic properties, but from substantial differences in heart rate of these two groups.
Key words. Aorta; elasticity; mechanical properties; Windkessel.

Arterial elasticity is an important determinant of haemodynamics in animals. The major arteries act as an elastic reservoir, storing blood transiently during systolic ejection, and providing flow to the periphery during diastole. In this way the elastic recoil of the artery wall converts the pulsatile output of the heart into a smoother flow in the peripheral circulation[1]. The elastic compliance of the arterial tree also reduces the pressure pulse and hydraulic impedance, and directly influences the speed of pressure wave transmission in the system.

In mammals the artery wall exhibits non-linear elasticity. This means that the vessel is compliant at low pressures,