Flexural Stiffness of Insect Antennae

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Antennae are important chemosensory and mechanosensory organs. An antenna will rotate or bend as forces act upon it, and therefore its sensory capabilities will be influenced by its mechanical properties (such as stiffness). From a mechanical point of view, insect antennae are cantilever beams (Fig. 1A); they fall into that category because they are attached at one end (to the head) and project into space without additional external support or buttressing. As with any cantilever beam, the longer an antenna, the more it will sag under its own weight (Fig. 1B). Some insects have extremely long antennae (e.g., those of longhorned beetles and adela moths), and yet they are held aloft by the insect and do not collapse onto the ground.

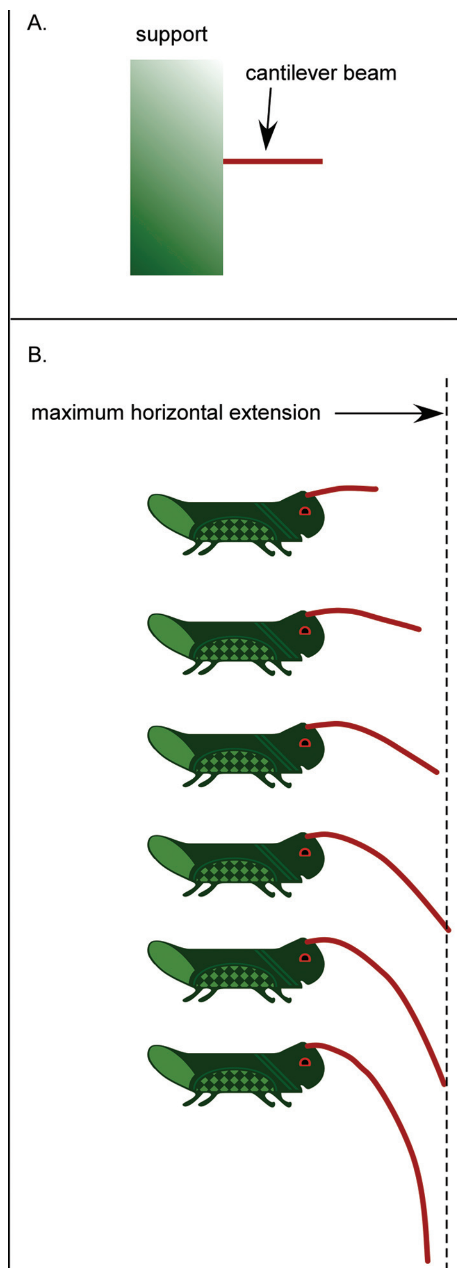

Fig. 1. A. A cantilever beam is a structure that is supported on one end. **B.** A cantilever beam (such as an insect antenna) will sag under its own weight as its unsupported length increases. A maximum possible horizontal extension (indicated by the dashed line) exists for a beam and will be larger for a beam of greater flexural stiffness.

Clearly, antennae must be stiff enough to support their own weight. But exactly how stiff should an antenna be? Insufficiently stiff antennae would flop around limply as an insect moves or turns its head, which could interfere with sensory functions. If antennae are too stiff, the rest of the attached insect will be jolted every time an antenna makes physical contact with something in the environment, much as a jousting knight may be knocked off his steed as his lance makes contact. Therefore, an antenna, at least at its distal end, needs to be sufficiently bendable so that the impact is largely absorbed by the bending of the antenna rather than by the jolting of the body.

The resistance to bending by a cantilever beam is quantified as "flexural stiffness." (Note that the convention is to use "stiffness" to describe material properties and structural properties; the meaning is usually clear by context.)

Flexural stiffness, a structural property, is written as EI because it is the product of two factors, E and I. E is the stiffness of the material (also called Young's modulus); a stiffer material will not stretch or compress as much as a less stiff material when pulled or pushed. The supporting material of an insect antenna is the cuticle of the exoskeleton. Stiffness (E) has been measured for some kinds of insect cuticle and ranges over an astonishing five orders of magnitude from the very stretchy locust ovipositor intersegmental membrane to the extremely stiff (60,000 times stiffer) locust apodeme (see Table 15.1 in Vogel 2003 for a compilation of E values). This variability in known cuticle properties makes it difficult to estimate *a priori* the stiffness of the cuticle in an insect antenna. Insect antennae are composed of a series of rigid segments and subsegments that are separated by the intersegmental (and intersubsegmental) joints at which the bending occurs. Therefore, it is the mechanical properties of the joints that primarily affect the bending behavior.

Although it should not be a surprise that the stiffness of a beam depends in part on the stiffness of the material used to construct the beam (and its joints), it may be a surprise that material stiffness is not the only determining factor in overall structural stiffness. The other factor that contributes to EI, I, describes how the material is

Fig. 2. A. Real antennae of a honey bee (*Apis mellifera*). **B.** A honey bee antenna is predicted to droop to the ground under its own weight if the length of the flagellum is four times longer as shown in this artist's depiction (assuming the same flexural stiffness as a real honey bee antenna; digital creation by J. Mellard).

arranged in space (the second moment of area), with each piece of material contributing more to stiffening if it is located farther from the axis of bending. Formulas for I are available for simple geometries (e.g. hollow cylinder, "I" beam) but not for the complex geometry of the folded cuticle at a joint in an antenna. A stiff antenna (large EI) may be the result of a thick cuticle (large I) or stiff cuticle (large E). As commonly found in biological systems, there are multiple possible routes to the same functional endpoint. In practice, E and I are extremely difficult to measure or estimate individually, particularly for such complex joints. However, if the mechanical behavior of the overall structure is of greater interest than individual estimates of E and I, this is convenient because the product, EI, may be measured more easily from the behavior of the structure, and it is the product that will be used for predicting a suite of other mechanical behaviors.

Flexural stiffness may be measured statically or dynamically. In static measurements, a known force is applied to an antenna, the resulting deflection measured, and this information is used to calculate the flexural stiffness. With a student, Jarad Mellard, I used this method to measure the flexural stiffness of individual honey bee antennae. We found that the flagella of honey bee antennae were about twice as stiff in the "down" direction, meaning that it is easier to push a honey bee antenna up (in a dorsal direction) than down (like gravity). With our estimate of flexural stiffness, we were able to predict the maximum length of a honey bee antenna before it would droop to the ground. Surprisingly, we found that an increase in length by a factor of only four would be sufficient (Fig. 2, Mellard et al. in preparation).

Dynamic measurements of flexural stiffness may be made by oscillating an antenna (such as on a shaker table), and I have started making such measurements on cockroach antennae with a colleague in Mechanical Engineering (Sara Wilson). It is clear from the resulting video images that the distal ends are much less stiff than the rest of the antennae, which is consistent with the tapering morphology of cockroach antennae.

Thus, flexural stiffness may change along the length of an antenna (cockroaches) and have different values when the antenna is loaded from different directions (honey bees), leading to subtleties in antennal sensory performance and mechanical behavior. Whereas some predictions of the mechanical behavior of antennae may be made by considering them from the vantage point of beam theory, much of "simple" beam theory explicitly assumes that any bending will be very small (appropriate for many applications in civil or mechanical engineering), and so is of limited applicability. Insect antennae regularly undergo very large bends and yet are able to return rapidly and elastically to their original shape, without a lot of springing back and forth. That is, although elastic, antennae are mechanically damped, which also means that an insect will not be shot backwards by elastic recoil after impact of its antennae with an object.

With new and exciting applications in robotics, the properties of these extremely versatile and sensitive sensory structures are generating interest in a number of laboratories. A compelling and informative introduction to biological structures as beams may be found in Vogel (2003).

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Appropriate shapes for bending beams in Fig. 1 were identified by tracing photographs of rubber rods bending under their own weight (McMahon and Bonner 1983, p. 144).

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