ANTENNAL BIOMECHANICS OF HOUSE CRICKETS (*ACHETA DOMESTICUS* L.)

BY

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Abstract

The structure of insect antennae is greatly influenced by the functional demands which the antennae fill, the environment in which they operate and the way these two factors interact with the biomechanical properties of the antennae. This study looks at such interactions in the House Cricket (*Acheta domesticus*) by examining the morphology, distribution of mass, and flexural stiffness of the antennae. In each case, the properties of the antennae were modulated by the need to have antennae that are long for mechanoreception, yet flexible enough to avoid damage. These properties are an important step towards understanding not only how insect antennae can be modified, but what implications these modifications have on the survival of the organism.

Introduction

Antennae are used by insects for a variety of tasks important to their survival. The effectiveness of a particular antennal design at a given task is limited by the morphology of the antenna and the way in which this morphology interacts with its physical environment. A good example of this is the plumose antennae of silkworm moths (*Bombyx mori* L.). The plumose antennae of this moth slow and spatially distort the air immediately in front of and moving through the spaces in the antennae.

This increases the probability of interception by the chemoreceptors located on the antennae and magnifies the patches of odorant molecules in the air (Loudon and Davis, 2005). While this particular morphology may be advantageous for chemoreception, it might also constrain the antenna's utility in other tasks, such as mechanoreception. Given this, understanding the biomechanics of insect antennae can be an integral part in understanding antennal form and function, as well as how these two factors relate to the environment in which antennae operate.

Previous studies on the mechanics of insect antennae have focused primarily on the importance of mechanoreception in auditory reception, flight, and gravity perception. Of these three, perhaps the oldest known and best studied is the importance of antennal mechanoreception in the audition of mosquitoes (Culicidae: Diptera) and fruit flies (Drosophilidae: Diptera).

The use of antennal vibrations for hearing in mosquitoes was first suggested by Johnston (1855), who described a chordotonal organ in the pedicel of the antennae. Johnston postulated that this chordotonal organ was capable of detecting vibrations of the flagellum which itself might be influenced by the vibrations of sound. The organ has since been named the "Johnston's organ" in honor of this discovery. Further work has validated his postulations by demonstrating the importance of the flagellum and Johnston's organ in mate finding (Clements, 1963). Work on hearing in fruit flies has demonstrated a similar scenario where the vibrations of the arista and funiculus (parts of the flagellum) are transmitted to the Johnston's organ (Göpfert and Robert, 2002).

Much as some flies use the Johnston's organ for audition, other insects have been demonstrated to use it to aid flight. An example of this are hawk moths (Sphingidae: Lepidoptera), which use the deflection of their flagella to detect Coriolis forces and improve the stability of their flight (Sane et al., 2007). Additionally, the use of flagellar vibrations has been shown to provide important information on air currents in both butterflies and locusts (Gewecke, 1975; Gewecke and Niehaus, 1981). In these cases, the mechanism of using the flagellum and Johnston's organ is similar to how flies use the same structures to hear, but the nature of the vibrations is different.

Blowflies (Calliphoridae: Diptera) and crickets (Gryllidae: Orthoptera) have also been shown to use deflections of their antennae to sense gravity (Horn and Kessler, 1975; Horn and Bischof, 1983). Unlike audition and sensing air currents, using antennae to sense gravity appears to rely on fringes of hairs at the pedicel-scape and scape-head joints. These fringes function to detect the deflections of the antennae caused by gravity.

Here we seek to examine the relationship between biomechanical properties and the environment in the antennae of the house cricket (*Acheta domesticus* L.). *Acheta domesticus* is a globally distributed insect with filiform antennae which are used for a variety of tasks including chemoreception, mechanoreception, thermoreception and hygroreception (Du Porte, 1920; Altner et al., 1983). In addition, *A. domesticus* is crepuscular, hiding in cracks and crevasses during the day and foraging in the evening. This creates a dichotomy in biomechanical function in

that the antennae must be stiff enough to support the length required for mechanoreception, but flexible enough to not be easily damaged while navigating their environment. Furthermore, cricket antennae play important roles in male dominance displays (Hofmann and Schildberger, 2001) and mate recognition (Balakrishnan and Pollack, 1997; Murakami and Itoh, 2003) in related species of crickets. In this case, any damage to the antennae can significantly reduce the reproductive potential of an individual. To understand how the characteristics of the antennae allow them to meet these opposing constraints, it is important to first understand the morphology, the distribution of mass, the manner in which the antennae bend, and the flexural stiffness of the antennae.

The filiform antennae of *Acheta domesticus* are characterized by a short scape and pedicel, with most of the antenna being taken up by flagellomeres (sclerotized annulations which comprise the flagellum) of fairly uniform thickness with no conspicuous constrictions at the joints (Metcalf et al., 1962) (Fig. 1). To understand how this morphology affects antennal mechanics, much more specific information is required. For instance, the width of flagellomeres along the length of the antenna can vastly affect the angle of bend of the antenna. Similarly, the number of the flagellomeres can also be a determining factor in the flexibility of the antenna.

The morphology of the antenna is linked to the distribution of mass along its length. For instance, a cylindrical antenna may have an even distribution of mass along its length, whereas the mass of a conical or tapering antenna is likely to be
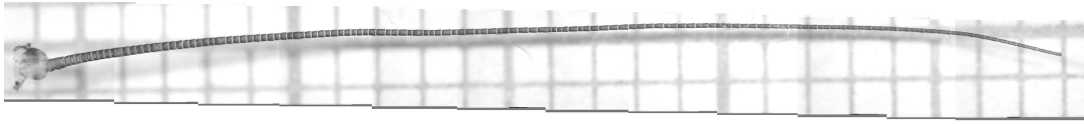
Figure 1: Overall morphology of the antenna from an adult female *Acheta domesticus*. Scale bar = 1mm.

weighted towards the base of the cone. Such differences will greatly affect the inertia and supportable length of the antenna.

The final project will be to examine the flexural stiffness (*EI*) of the antennae. Flexural stiffness is simply the amount to which a structure resists bending (see Vogel, 2003 for a review). This amount is calculated from two components: Young's modulus (*E*) and the second moment of area (*I*). Young's modulus itself represents the stiffness of the material the structure is composed of. In other words, it is the amount of force that is required to deform the material a given amount without regard for what shape the material is in. Since the shape of a structure can also affect its stiffness, the second moment of area is used to represent the shape of the structure and the distribution of that shape relative to the structure's neutral plane.

The flexural stiffness of an antenna can have a great effect on its structure and function, especially when the strength of the antenna is less than that of the structures it comes into contact with. As an antenna increases in stiffness, the risk of that antenna incurring damage as it moves past obstacles also increases (assuming constant failure strength) due to higher loading. Should the flexural stiffness be too low, then the antenna will be incapable of maintaining its shape under its own weight. Thus, knowing the flexural stiffness of cricket antennae and how it compares with other multi-jointed beams can yield valuable insight into the behavior of these antennae.

Materials and Methods

Morphological Characterization of the Antennae

The antennae were morphologically characterized in the following manner. Fifteen male crickets and 15 female crickets were killed by freezing them for 15-30 minutes. After the 15-30 minutes was over, the crickets were brought back up to room temperature for 5-10 minutes and weighed. Once their weight was recorded, both antennae were removed along with small attached portions of the head capsule to allow discrimination between right antennae and left antennae. The antennae were then placed in 50 μl pipets to protect the antennae and keep them straight, and then processed through an ethanol dehydration sequence (70%, 80%, 90%, 95%, 100%, 100% ethanol, remainder water). Following the dehydration sequence, the antennae were then immersed in Hemo-De for 24 hours, before being mounted on slides with Permount. Pictures of the antennae were then recorded using a Panasonic WV-CL700 video camera mounted on a dissecting microscope (Zeiss Stemi SV-6 with a 3.2 x objective and 0.63 x reducing lens).

For this magnification, a composite of approximately eleven adjacent still images was necessary to encompass the entire length of a single antenna, allowing a high resolution of approximately 9 microns per pixel. The still images were captured from the video recording using Snappy (New Generation Company) software. These slightly-overlapping images were pieced together in Canvas 8.0 (Deneba/ACD) and exported to Didger 2.0 (Golden Software, CO) for digitization. Four corners of each of the flagellomeres of the antennae were digitized (Fig. 2). From these points, the
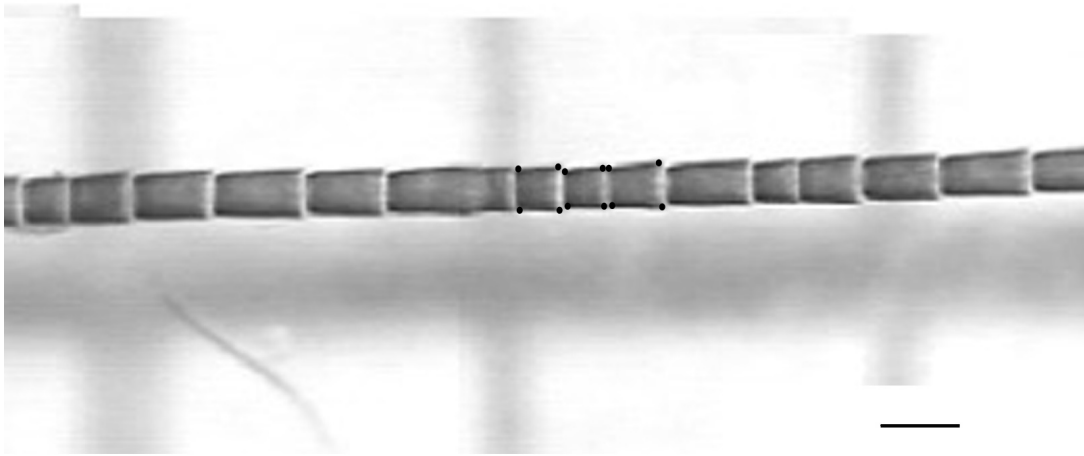
Figure 2: A section of an antenna showing the four points digitized on three adjacent

flagellomeres. Scale bar = 0.2 mm.

average length and width of the flagellomeres were calculated (Fig. 2) and analyzed using SAS software.

The length and width of the flagellomeres were then used to model the shape of the antenna. Due to the tapering nature of the antenna, a truncated cone was chosen as a basis for comparison. To do this, the length and width of the first five and last five flagellomeres of an antenna were used to predict the cumulative volume of a truncated cone with the same dimensions at the base and tip. Next, the length and width of the flagellomeres were used to find the cumulative length and volume of the flagellum.

Mass Distribution of Antennae

Six crickets (3 males, 3 females) with at least one antenna over 2.5 cm in length were chosen, placed in vials and refrigerated for anaesthetizing and slowing the crickets. After being cooled for approximately 15-30 min., the longest antenna was removed in its entirety, and weighed. The antenna was then cut into three pieces with the first cut being placed 1.0 cm from the base, and the next cut 2.0 cm from the base. The length of the most distal portion of the antenna was then recorded to the nearest mm. All three sections of the antenna were then weighed individually and analyzed with SAS software. This procedure resulted in minimal loss of fluid from the antenna prior to or during the process of measurement.

EI measurements

A total of 40 crickets (20 male and 20 female) were used to obtain EI measurements. Only the right antennae of adult crickets were used so as to avoid any possible difference in flexural stiffness between right and left antennae. Once a cricket with an antenna measuring approximately 2 cm or more in length was selected, it was placed in a container and immobilized using carbon dioxide for at least 20 minutes. This process appeared to leave the crickets unconscious for a limited amount of time as all of the crickets started moving appendages approximately 10 minutes after being returned to air. Once the cricket was immobilized, it was removed and placed in a plastic holder. The left antenna was removed and the right antenna was affixed in an anterior direction by epoxy. To accomplish this, epoxy was applied to encompass the entire head capsule, as well as covering the scape and pedicel. The epoxy was then left to cure for the next 5-6 hours or until completely solid. This amount of time was necessary for the epoxy to completely cure and prevent the affixed portions of the antennae from moving during the testing phase. By the time of testing, the crickets responded normally to stimuli. Chilling in the freezer was not used for immobilizing crickets for these measurements because we found that the tips of the antennae appeared to be less stiff after exposure to freezing temperatures (the end of the antennae drooped distally).

The force measurements were made using a Omega strain gage force transducer which was constructed out of two 120-ohm strain gages (KFG-IN-120-C1-11L1M2R) glued on spring steel from Small Parts Inc.(FSS-05/4-6, 0.127 mm thick). A small wire was removed from a multi-stranded insulated electrical wire

Beldon PVC hook-up wire 20 awg 10 strands of #30 (0.05 mm^2 tin and copper) and one end of the wire was then glued to a hole in the end of the spring steel. The other end of the wire was fashioned into a hook. The force transducer was connected to a bridge (BCM-1 from Omega) and then to an amplifier (DMD-465 Bridgesensor from Omega), before being input directly into PowerLab 2/20 (ADI Instruments). Output from the force transducer was recorded using Chart 5 for Windows (ADI Instruments). Before recording, the force transducer was calibrated using a 385 µN weight. The plastic holder was then attached to a micromanipulator so that the antenna was positioned just above the hook of the force transducer (Fig. 3).

Once the force transducer was calibrated, the antennae were then moved in a horizontal plane using a micromanipulator until the hook of the force transducer was located 5 mm away from the head capsule of the cricket (preliminary results indicated that this was the furthest point from which force measurements could be obtained). The output from the force transducer was recorded for approximately 30 sec (to determine the baseline zero) and the set-up was photographed using the still image function of a Panasonic PV-GS400 digital video camcorder. The antenna was then moved down 0.5 mm using a micromanipulator, pulling the hook of the force transducer. The force was again recorded for 30 sec and an image was taken to determine the deflection of the antenna in response to that force. This process was repeated three more times until the antenna had been moved 2.0 mm from its initial position.
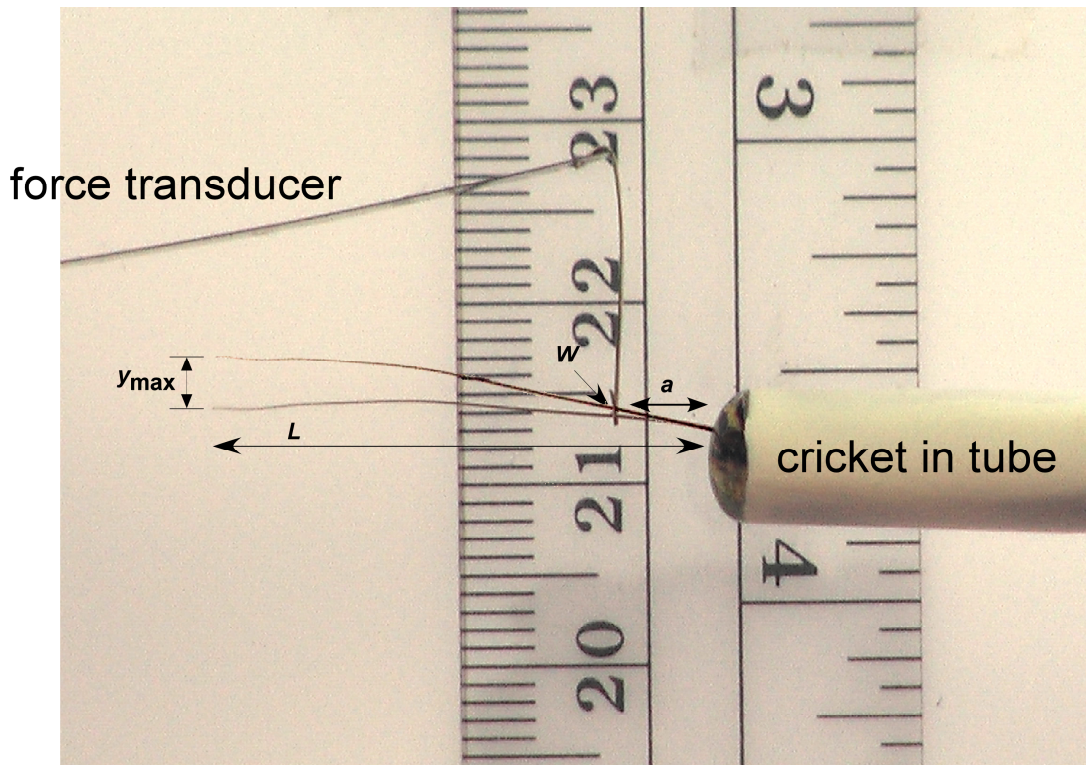
Figure 3: Showing the set-up used to measure the EI of the cricket antennae.

The images were digitized using Canvas 8 (Deneba) to determine the deflection of the antenna. Data taken from deflections between 1 and 4 mm (measurements outside of this range were discarded) were then inserted into the following equation taken from (Roark, 1943):

$$EI = 1/6 \times W/y_{max} \times (3a^2L-a^3)$$

Where W was the average force value over the 30 sec interval, y_{max} was the deflection of the antenna, a was the distance from the force transducer hook to the head capsule and L was the length of the antenna (measured to the nearest mm). These measurements were calculated with the cricket oriented with the ventral side up (so that the force was applied from a dorsal direction) and dorsal side up (force applied ventrally). This process was repeated three times per cricket and the results were then averaged and analyzed with SAS software. No trend in successive measurements was noted.

Results

Antennal Morphology

The crickets (*Acheta domesticus*) used in this study possessed filiform antennae ranging between 2.5 cm and 3.5 cm in length (unless broken). The scape of the antenna is greatly enlarged and dorsoventrally compressed compared to the shape

of the other antennal segments. This shape, combined with the presence of the fastigium, limited the horizontal movement of the segment. Similarly, the scape-pedicel joint also formed a hinge which limited vertical movement. The pedicel itself is much smaller than the scape and resembles an elongated flagellomere.

The number of flagellomeres found in an antenna varied greatly, with the largest number of flagellomeres on a single antenna being 293 and the least being 28. The average number of flagellomeres for all antennae used in this experiment was 163 (standard deviation of 62) with no significant differences between sex for either the right or left antennae (1-way ANOVA, $p = 0.1023$, $p = 0.2795$, respectively).

For males, the length of the flagellomeres decreased slightly along the length of the antenna following the equation $y = -0.0004x + 0.1443$ ($r^2 = 0.4278$) where y is flagellomere length (mm) and x is flagellomere number (counting from the proximal end). The equation for flagellomere length for females was $y = -0.0004x + 0.1618$ ($r^2 = 0.3737$). When both sexes were combined, it yielded the equation $y = -0.0004x + 0.1536$ ($r^2 = 0.3997$). The variation (calculated as the percent change) in flagellomere length between successive flagellomeres was found to be significantly different between sexes (Paired t-test, $p = 0.0261$ for left, $p = 0.0021$ for right), such that males were more variable; however, neither the number of flagellomeres, nor total length of the flagellum was found to be significantly different between the sexes.

The width of the flagellomeres was significantly less variable than the length (comparing average percent change in successive flagellomeres, paired t-test, $p < 0.0001$). The width of the flagellomeres decreased logarithmically further out from

the head capsule following the equation $y = -0.0489 \ln(x) + 0.3178$ ($r^2 = 0.9313$)

where y is flagellomere width (mm) and x is flagellomere number (counting from the

proximal end). The equations describing the width of the flagellomeres along the

length of female ($y = -0.0487 \ln(x) + 0.3191$) and male ($y = -0.0488 \ln(x) + 0.3156$)

antennae did not significantly differ.

The dimensions of the truncated cone predicted from average widths of the

first five and last five flagellomeres followed the equation $y = 2 \times 10^{-05}x^3 - 0.0014x^2 +$

$0.0394x$ where y is the cumulative volume (mm^3)and x is the cumulative length

(mm). This differed slightly from the actual cumulative volume and length based on

measurements from all flagellomeres, each of which was treated as a circular

cylinder, which followed the equation $y = 5 \times 10^{-05}x^3 - 0.002x^2 + 0.0355x$ ($r^2 = 0.9972$)

(Fig. 4).

Antennal Mass

Among the six antennae used in this study, the average mass of the whole

antenna was 0.60 mg (standard deviation = 0.05). When sectioned into three pieces,

the segment closest to the head capsule comprised an average of 65.0% (0.42 mg) of

the mass of the entire antenna. The mass of each successive section of the antennae

decreased so that the second section comprised 21.3% (0.14 mg) and the third 13.6%

(0.09 mg) (Table 1). On average, the sum of the mass from each section differed

from the mass of the whole antenna by 0.05 mg (14.8%). This distribution in mass

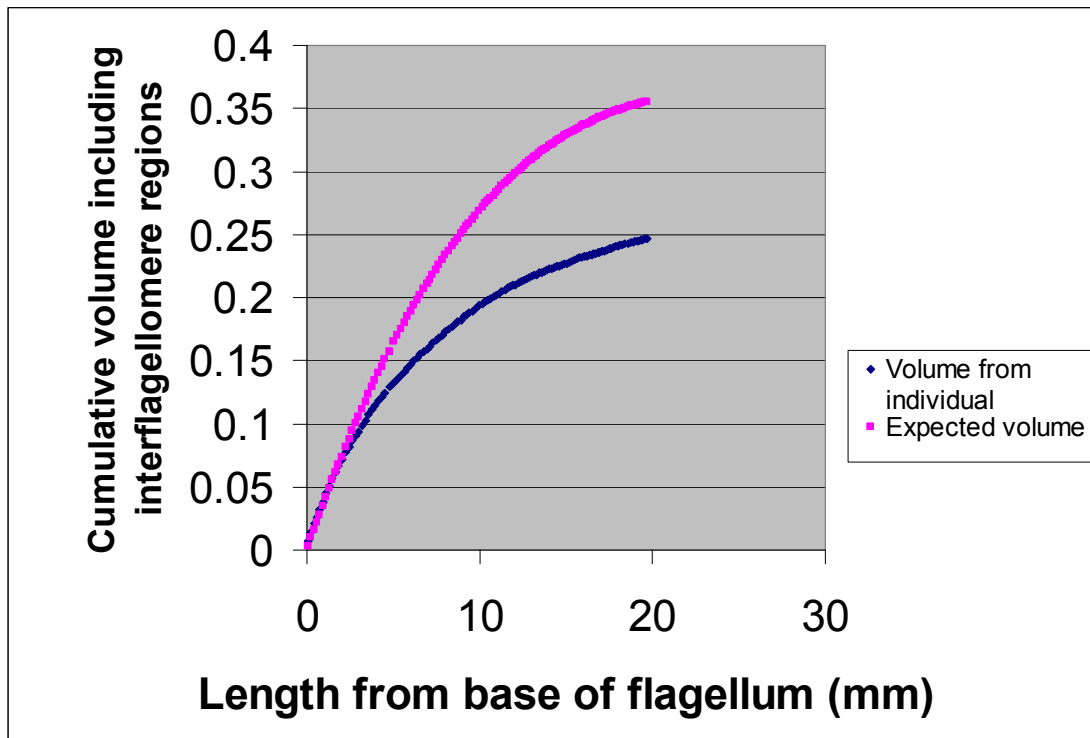followed the quadratic equation $y = 5E^{-05}x^3 - 0.0029x^2 + 0.0679x - 0.0088$

Figure 4: Comparison of predicted volume based on approximating the shape as a truncated cone and observed volume of the flagellum.

Table 1: Comparison of the mass of the sections of antennae (mg)						
Individual	First cm	Second cm	Remaining	Sum of Parts	Whole antenna	Difference	Percentage
F1	0.42	0.18	0.1	0.7	0.66	0.04	6.0606
F2	0.38	0.07	0.07	0.52	0.63	-0.11	17.4603
F3	0.47	0.15	0.1	0.72	0.57	0.15	26.3158
M1	0.37	0.12	0.08	0.57	0.58	-0.01	1.7241
M2	0.37	0.13	0.07	0.57	0.53	0.04	7.5472
M3	0.49	0.19	0.11	0.79	0.61	0.18	29.5082
Averages	0.416667	0.14	0.088333	0.645	0.596667	0.04833	14.7694
St. Dev.	0.052789	0.043818	0.017224	0.106348	0.046332	0.106097	11.454

($r^2 = 0.823$) where y is the mass (mg) and x is distance along flagellum (mm).

EI of the Antennae

Table 2 summarizes the data set (19 males, 19 females). Two outliers (identified by values greater than two standard deviations from the mean) were discarded (ADM13: 19.429 nNm^2 for dorsal up, 17.215 nNm^2 for ventral up; ADF17: 3.700 nNm^2 for dorsal up, 3.425 nNm^2 for ventral up). ANOVA was applied to determine whether the stiffness of the antennae was different between males and females, and depending on whether the force was from a ventral direction ("dorsal up") or dorsal ("ventral up"). The flexural stiffness differed significantly between males and females when the force was applied from the ventral direction (1-way ANOVA p = 0.0052), but not from the dorsal direction (p = 0.1106). There was no significant difference in flexural stiffness whether the force was from a dorsal or ventral direction for either females or males (paired t-test: females, p = 0.8479; males, p = 0.1404).

Discussion

The antennae of *A. domesticus* are characterized by two hinge joints (head-scape and scape-pedicel) mounted at orthogonal angles in the vertical and horizontal planes. The flagellum comprises the majority of the length of the antenna and is

Table 2: Results of the EI measurements.

Sex	Orientation	Sample Size	Mean nNm^2	Standard Deviation nNm^2	Maximum nNm^2	Minimum nNm^2
Female	Dorsal Up	19	13.037	4.331	21.913	7.157
	Ventral Up	19	12.812	4.632	21.361	5.051
Male	Dorsal Up	19	9.462	3.376	15.816	4.498
	Ventral Up	19	10.660	3.386	16.993	4.431

characterized by a large number of annulations. This morphology is consistent with what has been found in *Gryllus campestris* and may allow for greater ease in horizontal tracking movements (Honegger, 1981).

In our experiments, we found that the first centimeter of the antenna (proximal to the base) comprised almost two-thirds of the mass of the entire antenna. Additionally, the width of the flagellomeres decreases along the length of the flagellum. While this change only amounts to a 0.25 mm decrease along the length of an antenna 2.5 cm long, it still represents enough of a change as to play a role in this distribution of mass. Since most of the mass is distributed close to the base of the antenna, this allows the antenna to have a center of mass close to the base of the antenna. This allows for greater dexterity in moving the antenna.

Corroborating this distribution of the mass is the change in volume of the flagellum along its length. The volume of the flagellum changes in a non-linear fashion similar to what one would expect of a truncated cone. However, the cumulative volume of the flagellum is lower than one would predict if one were to model the dimensions of a truncated cone from the first five and last five flagellomeres. This difference appears to be due to a curvilinear decrease in flagellomere width (Fig. 5).

This tapering may also be the result of a biomechanical trade-off with regards to the width of the flagellomeres. While wider flagellomeres allow greater dexterity and support for moving the flagellum, wider flagellomeres also decrease the angle of
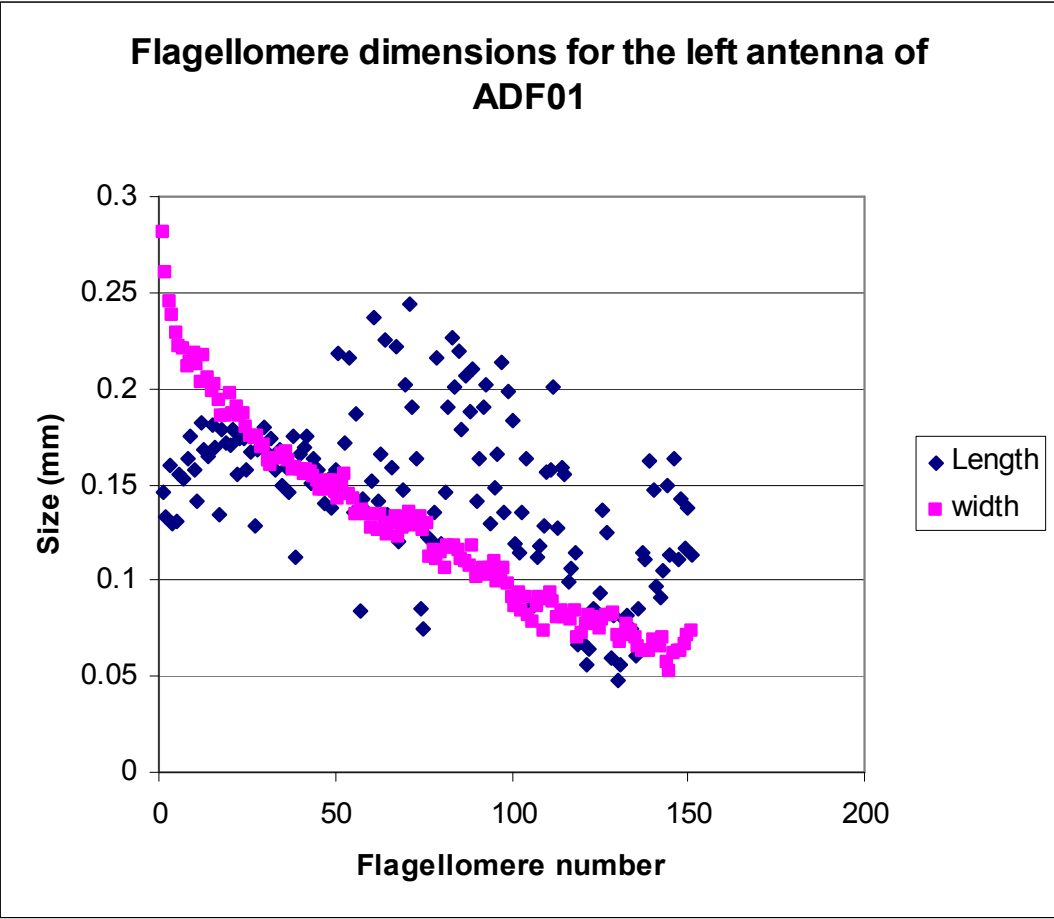
Figure 5: Dimensions of the flagellomeres for an individual antenna from an adult female.

bend between flagellomeres (Fig. 6). An increase in the width of flagellomeres (without a corresponding increase in the length of membranous joint between adjacent flagellomeres) will lead to a decrease in the maximum angle of articulation. As such, while wide flagellomeres at the base may provide for increased support and dexterity, a rapid decrease in the width of the flagellomeres could allow for greater flexibility further away from the head.

A similar trade-off may exist in the length of flagellomeres. While increasing the length of the flagellomeres would not affect the angle of bend between flagellomeres, the added length would decrease the number of points of articulation in a given unit of area. Thus, unless this was compensated for in some other fashion, increasing the length of the flagellomeres would result in decreasing the angle of bend an antenna is capable within a particular space (Fig. 6). The observed length of the flagellomeres was much more variable than expected. Unpublished data (Miller and Loudon, Pers. Comm.) from the American Cockroach (*Periplanata americana*) shows that the flagellomeres increase in length from the base to the tip of the antenna in a "s"-shaped manner. The length of the flagellomeres in *A. domesticus*, on the other hand, varies greatly from one flagellomere to the next due to the interspersing of short annuli amongst longer annuli (see Fig 7). This pattern of short and long annuli does not appear to be consistent between antennae, and the developmental mechanism of this pattern is unknown.

Previous studies on the stiffness of *Locusta migratoria* (Orthoptera: Insecta) and *Apis mellifera* (Hymenoptera: Insecta) antennae have demonstrated a difference
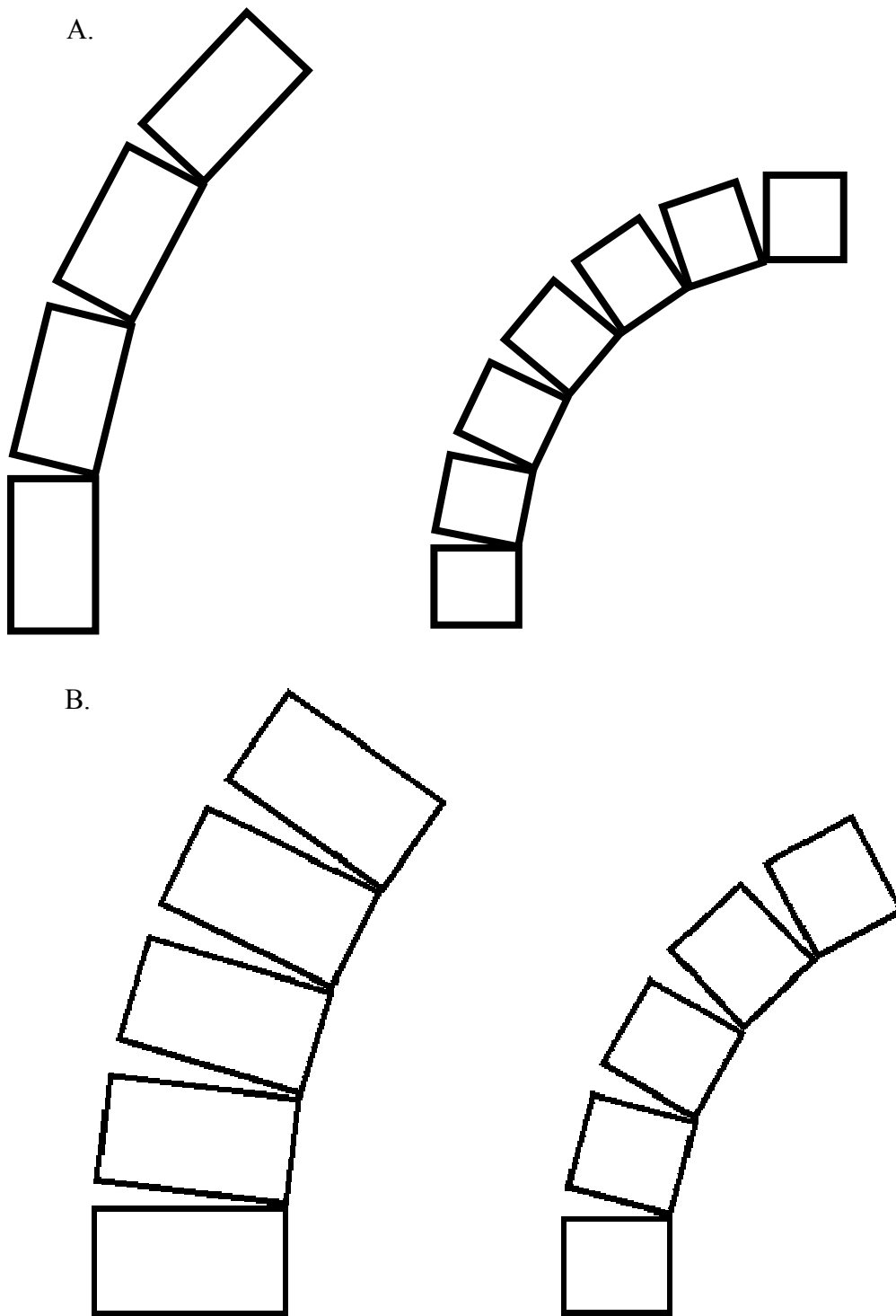
Figure 6: Effect of flagellomere dimensions on an antenna's angle of bend. *A*. Longer flagellomeres with the same angle of bend between flagellomeres, but fewer points of articulation in a given unit of area. *B*. Wider flagellomeres with the same number of articulations, but smaller angle of bend between flagellomeres.

Figure 7: Part of a single antenna showing the juxtaposition of shorter annuli amongst longer ones.

in stiffness based on whether the force was applied from a dorsal to ventral or a ventral to dorsal direction (Heran, 1959; Gewecke and Heinzel, 1980). In both cases, the antennae were stiffer when bent in a ventral to dorsal direction. Our data did not demonstrate such a relationship, though there were nonsignificant trends in opposite directions for the two sexes (Table 2). That *Acheta domesticus* antennae do not demonstrate a directional difference in stiffness is probably due to the differences in locomotion. Both *Locusta migratoria* and *Apis mellifera* spend a significant amount of time flying. This requires their antennae to be capable of maintaining position while exposed to frontal air currents. *Acheta domesticus*, on the other hand, is almost entirely cursorial. As such, it is not necessary to have a directional bias in antennal stiffness.

Furthermore, the antennae of *Acheta domesticus* were found to be much stiffer than those of *A. mellifera*. Mellard and Loudon (Pers. Comm.) found a flexural stiffness of 62 pNm^2 for a dorsal to ventral direction, and 103 pNm^2 for the ventral to dorsal direction. The stiffness measured in both directions are approximately 100 times smaller than the forces calculated for *Acheta domesticus*. This difference in stiffness is probably needed to support the greater length of *A. domesticus* antennae. That said, the exact degree of this difference depends on the point at which the flexural stiffness is measured on the antennae of *A. domesticus*.

As mentioned previously, flexural stiffness is calculated from Young's modulus and the second moment of area. Since the flagellomere width decreases along the length of the flagellum, the second moment of area should decrease

correspondingly. As such, it is important to note that the precise values for flexural stiffness are only valid for this particular point on the antenna (approximately 0.5 cm away from the head capsule.

The flagellum of an insect's antenna can play a large role in locomotory behaviors such as escape (Camhi et al., 1978, Ye et al., 2003) and high-speed running (Camhi and Johnson, 1999). Each of these cases (flagellomere morphology, distribution of mass, and flexural stiffness) show a trade-off between the antenna's necessity for length, and the necessity for flexibility. This trade-off is an especially important one due to the role of the flagellum biomechanics in locomotion. The use of flagella for navigation and orientation has been shown in a couple of different insect groups (Colorado Potato Beetles: Pelletier and McLeod, 1994; cockroaches: Camhi and Johnson, 1999). Any modifications to the structure or biomechanics of the flagella could impact the insect's ability to navigate through their environment. As such, it is important not only to understand how an antenna can be modified, but also the impact these modifications can have to the survival of the organism.

Acknowledgments

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