Bumblebee hair motion in electric fields

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Abstract. Bees have been observed to detect and learn the presence of weak electric fields in various behavioural experiments in the lab. The electro-sensitivity of bumblebees has also been suggested to be important for pollination. However, the structure and function of electro-sensory organs are yet to be described. Bees, like other arthropods, are known to have evolved various mechanoreceptors. Antennae and hairs have mechanosensory functions and have been shown to respond to weak electric fields. Current proposals posit that hairs and antennae can act as electromechanical sensors. To investigate this hypothesis, the mechanical response of bumblebee hairs stimulated by an electric field was measured using microscanning laser Doppler vibrometry. Hair vibration velocity is shown to be proportional to charge triboelectrically deposited on the bee and the effect of polarisation charge is seen to be negligible. Hair motion due to acoustic stimuli is also measured and compared to hair electromechanical response. Preliminary results show that the electro-sensitivity of charged bee hairs is comparable to hair sensitivity to acoustic stimuli.

1. Introduction
Bees have been shown to respond to electrical cues in behavioural experiments [1, 2]. In natural environments, it is suggested that they use electrical information for foraging [3] and communication [2, 4].

Arthropods possess mechanosensory antennae [5] and hairs [6] that respond to acoustic cues and fluid flow [5, 6] as well as electric fields [7, 2, 8]. The mechanosensory response of hairs and antennae has been characterised in detail using fluid flow and acoustic stimuli [6]. Comparatively, little is known about the sensitivity of hairs or antennae to electrical stimuli. The work by [7] demonstrates basic characteristics of bumblebee hair electromechanosensing. Notably, that hair movement elicited by an external electric field is much larger in charged than electrically neutral bumblebees.

Here, the physical mechanism for electromechanical actuation of bumblebee (Bombus terrestris) hairs is investigated in more detail. Using laser Doppler vibrometry (LDV), the vibration velocities of individual hairs on bumblebees were measured in response to an electric field. The influence of charge on hair motion was characterised by varying the net charge on the bee. To compare electro- to acousto-mechanical coupling, hair vibration velocity was also measured under acoustic forcing.

2. Methods
All experiments were performed on freshly killed bumblebees. For LDV measurements (Polytec PSV500 with close-up attachment, Polytec Germany), the laser spot (diameter 5 μm) was focused and positioned near the distal end of a single hair for each animal.
2.1. Relation between bee charge and hair vibration
Each bee was held in a plastic sleeve and placed on a wooden platform on a grounded table (ground plane in Figure 1) along with the laser, allowing charge to leak from the bee during the LDV measurements. Charge was deposited on the bee by contact with a nylon ball. Bee charge was measured using a Faraday pail (JCI 147, Chilworth UK).

External electric field was applied via wires held ∼ 1.5 cm apart with the sample in between. The wires were connected via shielded cable to the output of a signal generator producing a 132 Hz, 9.5 V sinusoid. The amplitude is representative of electric field ∼ 2 cm from a floral surface (up to 1000 V/m [1]).

2.2. Comparison to acoustic coupling
To compare electro- and acousto-mechanical coupling, each bee was slightly charged (∼ 4 pC) as per [7] and placed on insulated mounting to reduce charge leakage. Again, pure tone signals (0.75–2.5 kHz, 2–360 V) were produced by a signal generator. These were routed to an in-ear headphone speaker. To generate a point acoustic source with significant particle velocity component, the speaker output was directed through flexible tubing to a tapered point. Electrical stimuli were generated by connecting the signal generator output directly to a rounded metal pin. Distance between the stimuli sources and the sample was 7.5 mm.

Each sample was exposed to varying levels of acoustic and electrical stimuli. Exact sound pressure (Brüel & Kjær type 4138) and velocities (as per [9]) at the sample location were measured after each experiment - the sample was removed and the acoustic stimuli generated again at the same input signal level.

![Figure 1](image.png)

Figure 1. Schematic of experimental setup for (a) charge decay and (b) acoustic comparison experiments.

3. Results
Charge on each bee was measured shortly (∼ 2–3 minutes) before and after LDV measurement - ranging from 200–400 pC initially and 0–15 pC finally. Additionally, charge leakage over time was measured from separate bees mounted similarly (Figure 2a).

Figure 2b shows a representative spectrum of hair vibration velocity, ν. The broadband noise with maximum magnitude at ∼ 300 Hz varies within an order of magnitude between measurements. There is an amplitude peak at the frequency of the generated signal (132 Hz) that varies between bees (154.9–5604 nms⁻¹). Figures 2c and d show the time-resolved amplitude and phase of ν at this frequency; a decaying amplitude with constant phase is seen.

Measured hair response to electrical and acoustic stimulus exhibited similarity so that they cancel when superposed in anti-phase. Figure 3a shows ν when both stimuli were applied with varying relative phase. When they are in anti-phase, destructive interference occurs producing
Figure 2. Charge leakage and electromechanical response of bumblebee hairs. (a) Charge leakage (bees 1–5); (b) Spectrum of hair vibration velocity (bee 6); (c) Normalised $|\nu|$ at stimulus frequency (bees 6–10); (d) Vibration velocity phase at stimulus frequency (bees 6–10).

Figure 3. Electric vs acoustic coupling. (a) Cancellation of hair vibration response to electric stimulus by acoustic stimulus; (b,c) Electric stimulus amplitude compared to sound pressure and particle velocity needed to generate similar $|\nu|$ (within 5%). Noteworthy is the interindividual variation in the electro-acoustic gain (slope) of the hair response.

4. Discussion

4.1. Electromechanical actuation scales with charge

Electrostatic forces scale with charge and electric field according to Coulomb’s law ($\vec{F} = q\vec{E}$). For an insulator such as bumblebee hair, net charge can be gained from external sources
or polarisation charge induced by the electric field. In the latter scenario, polarisation is proportional to $\vec{E}$ itself so that $\vec{F} \propto \vec{E}^2$ and the hair torque generated would be doubled in frequency to $\vec{E}$. The measurements made (Figure 2b) show that the double frequency component (polarisation effect) is below the noise floor of the measurement, much smaller than the signal at the stimulus frequency (net charge effect). Geometry may play a role - for a horizontal electric field acting on an upright hair, the equal and opposite charges induced on the hair produce opposing forces. However, it is unlikely that the hair and electric field in the experiments are perpendicularly oriented.

Further, $|\nu|$ at the stimulus frequency shows a trend characteristic of charge decay in similarly mounted samples (compare Figures 2a and c). The charges applied here (0–400 pC) are representative of in vivo net charge on bumblebees ($\sim32$ pC, [7]), suggesting that electrical force on bumblebee hairs (and hence electromechanical actuation) in nature will be due to charge accumulation rather than polarisation charge.

4.2. Comparison with acoustomechanical actuation

Conventionally, hairs are deemed to be mainly sensitive to the particle velocity component of acoustic stimulus which is subject to various factors, e.g. geometry, frequency and distance to the source [10]. The excitation is also influenced by hair characteristics such as geometry, mass and stiffness. The relationship between equivalent electrical and acoustic stimulus is seen to be variable (Figure 3), likely reflecting the variability between the samples. Nevertheless, the results demonstrate that hair motion due to naturally occurring levels of hair charge and electric field is significant relative to motion excited by ambient sounds.

5. Conclusions

The velocity of Bumblebee hairs in the presence of an applied electric field was measured using LDV. The results show that (1) electromechanically actuated motion of bumblebee hair is proportional to net charge on the bee and (2) electric force can be a significant proportion of the total forces acting on the bumblebee hair in ecologically relevant scenarios. It follows that the mechanical effect of ambient electric fields on bumblebee hairs will be larger in conditions conducive for charge accumulation and vice versa. This finding is pertinent to bumblebee behaviour regardless of the biological function(s) of bumblebee hair since the electrical force can be either signal or noise.

References

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