

# Mechanosensory hairs in bumblebees (*Bombus terrestris*) detect weak electric fields

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**Bumblebees (*Bombus terrestris*) use information from surrounding electric fields to make foraging decisions. Electroreception in air, a nonconductive medium, is a recently discovered sensory capacity of insects, yet the sensory mechanisms remain elusive. Here, we investigate two putative electric field sensors: antennae and mechanosensory hairs. Examining their mechanical and neural response, we show that electric fields cause deflections in both antennae and hairs. Hairs respond with a greater median velocity, displacement, and angular displacement than antennae. Extracellular recordings from the antennae do not show any electrophysiological correlates to these mechanical deflections. In contrast, hair deflections in response to an electric field elicited neural activity. Mechanical deflections of both hairs and antennae increase with the electric charge carried by the bumblebee. From this evidence, we conclude that sensory hairs are a site of electroreception in the bumblebee.**

electric fields | bees | behavior | sensory biology

**E**lectroreception is common in aquatic animals. First discovered in sharks (1), electroreception has also been found in rays (2), amphibians (3), teleost fish (4, 5), dolphins (6), platypuses (7), and echidnas (8), which use electrosensory organs in their snout to detect prey in wet soil.

The first specialized electrosensory structures discovered were the “ampullae di Lorenzini” (9). Ampullae are small tubular cavities containing an electrolytic jelly (2), which maintains the same electric potential as the water immediately adjacent. In sharks and rays, differences in electric potential between the inside of the animal and the jelly are transduced by epithelial cells (10), where negative deviations in potential are excitatory whereas positive ones are inhibitory (11). Teleost fish have independently evolved electroreceptors that are excited by positive voltages and inhibited by negative voltages (11). This general mechanism for electroreception has evolved independently in several animal lineages (12, 13).

Ampullary electroreception requires the presence of an electrically conductive medium. Even in terrestrial animals such as the platypus and echidna, electroreceptive organs need to be submerged in water or surrounded by damp or humid substrates to function (7, 8). In contrast, bees detect weak electric fields in dry air, an electrically insulating medium. Bumblebees detect the presence of floral static electric fields (14), and honeybees detect oscillating fields associated with their waggle dance (15). In air, ampullary electroreceptors are ineffective because of an absence of conductive medium between the sensory organ and the environment. We thus investigate the possibility that electric fields instead exert forces on charged, mechanosensory structures on the bee: hairs and antennae.

To investigate electroreception in air, we use noncontact laser Doppler vibration measurements and electrophysiology. We test two hypotheses: First, bumblebees use their antennae to detect electric fields. This hypothesis is supported by evidence that honeybee antennae deflect in response to electric fields analogous to those produced by conspecifics performing the waggle dance (15). Second, bumblebees use mechanosensory hairs to detect electric fields. In support of that hypothesis is the rich literature on arthropod sensory hairs detecting small forces associated with fluid flow and sound particle velocity (16). We find that electric fields of

ecologically relevant magnitudes cause motion in both the antennae and body hairs, but only hair motion elicits a commensurate neural response. From these data we conclude that hairs are used by bumblebees to detect electric fields.

## Results

**Bumblebee Hairs and Antennae Mechanically Respond to Electric Fields.** The motion of the antennae and sensory hairs in response to applied electric fields was measured by using a laser Doppler vibrometer (LDV) (Fig. 1). LDV measures the vibrational velocity ( $v$ ) of structures undergoing oscillations, which was transformed into displacement ( $x$ ) and angular displacement ( $\theta$ ) (*SI Results*). “Displacement” is the absolute motion of the structure, whereas “angular displacement” is the motion of the structure in relation to its length. Angular displacement is proportional to the strain on the mechanoreceptors innervating the joint, either at the flagellum-pedicel joint of the antenna (Johnston’s organ) or the base of the hair.

**Electromechanical Responses to Broadband Electric Field Stimulation.** A 400 V<sub>pp</sub> sinusoidal frequency sweep from 10 Hz to 10 kHz (sweep duration: 0.64 s) was applied to a steel disk, 1 cm from the hair or antenna. Alternating electric fields were used because they cause steady-state velocity responses suitable for LDV. For each bee ( $n = 10$ ), the responses of two hairs and both antennae were recorded (Fig. 1), in both a charged and an uncharged preparation (Figs. S1–S3). The resonant frequency was the frequency of maximum response amplitude. The mean resonant frequency for hairs was  $3.8 \pm 0.2$  kHz and  $1.1 \pm 0.3$  kHz for antennae (Table 1).

## Significance

Electroreception in terrestrial animals is poorly understood. In bumblebees, the mechanical response of filiform hairs in the presence of electric fields provides key evidence for electro-sensitivity to ecologically relevant electric fields. Mechanosensory hairs in arthropods have been shown to function as fluid flow or sound particle velocity receivers. The present work provides direct evidence for additional, nonexclusive functionality involving electrical Coulomb-force coupling between distant charged objects and mechanosensory hairs. Thus, the sensory mechanism is proposed to rely on electromechanical coupling, whereby many light thin hairs serve the detection of the electrical field surrounding a bumblebee approaching a flower. This finding prompts the possibility that other terrestrial animals use such sensory hairs to detect and respond to electric fields.

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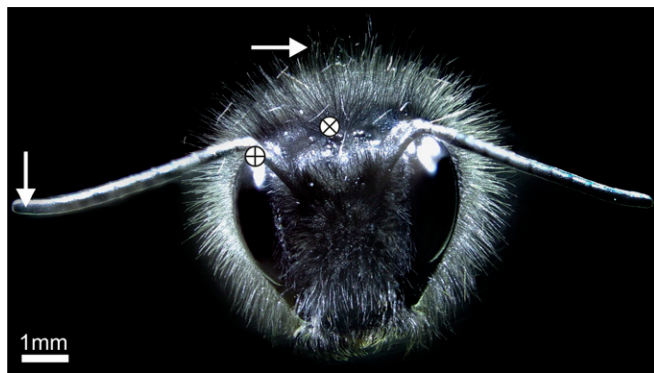
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**Fig. 1.** Bumblebee covered in body hairs. The white circle containing a plus (+) denotes electrode insertion points in the antennae. The white circle containing a cross (x) denotes approximate electrode insertion points for hair recordings. White arrows show the laser focal position for hair and antennae LDV recordings.

Hairs and antennae both move in response to electric fields. Hairs respond with significantly greater maximum and median velocity ( $v_{\max}$ ,  $v_{\text{median}}$ ) than the antennae (Fig. 2A). The difference between maximum displacement ( $x_{\max}$ ) of hairs and antennae is not statistically significant, although hairs respond with significantly larger median displacement ( $x_{\text{median}}$ ) (Fig. 2A). The tips of hairs and antennae move a similar absolute distance in response to electric fields at their respective resonant frequencies, although the hairs move more in response to spectrally broad electrical stimulation (Fig. 2B). Because hairs are much shorter than antennae, the maximum and median angular displacement ( $\theta_{\max}$ ,  $\theta_{\text{median}}$ ) of hairs is significantly greater than that of antennae (Table 1 and Fig. 2C). The velocity of the hair is an order of magnitude greater than that of the antennae. Both hairs and antennae move like a stiff rod, pivoting the base where mechanosensory neurons are located. The absence of bending is revealed by the invariant phase response between the stimulus and the displacement at resonance (Fig. S3).

**How Sensitive Is the Electromechanical Response?** To determine the minimum stimulus voltage generating a measurable mechanical response, spectrally pure sinusoidal voltages are applied to the stimulus delivery disk. To evaluate maximal sensitivity, stimuli were applied at the resonant frequency and at a second nonresonant frequency of the hair or antenna. The voltage at which the measured vibrational velocity is statistically distinguishable from thermal noise ( $U_{\min}$ ) is recorded for hairs and antennae in both charged and uncharged states.

Throughout the entire range of test conditions and stimulus voltages, the vibrational velocity of the hairs was an order of magnitude greater than that of the antennae (Fig. 3C and D).  $U_{\min}$  was

also lower for hairs than for antennae, indicating a higher sensitivity to electric fields (Table 2).  $U_{\min}$  for charged hairs was 25 mV for both resonant and nonresonant stimuli.  $U_{\min}$  for charged antennae was 500 mV at resonance and 10 V off resonance (between 20 and 400 times greater than the hair). Only when the bee's charge was deliberately set to zero, did the antennae respond to a lower voltage than the hair. In natural free-flight situation, however, bees are only rarely found with zero charge (15, 17).

**Minimum Electric Field Strengths Required to Elicit Electromechanical Responses.** To quantify the electric field associated with our stimuli and to evaluate its distance of action, finite element analysis (FEA) was used to compute field geometry and strength  $E$ . The computed field was evaluated at the location of the sensor (1 cm axial distance from the disk) for various disk voltages. The minimum electric field strength ( $E_{\min}$ ) required to produce mechanical motion in charged hairs is  $0.77 \text{ V}\cdot\text{m}^{-1}$  for resonant stimuli and  $61 \text{ V}\cdot\text{m}^{-1}$  for nonresonant stimuli. For antennae,  $E_{\min}$  is much higher ( $15.3 \text{ V}\cdot\text{m}^{-1}$  for resonant stimuli and  $306 \text{ V}\cdot\text{m}^{-1}$  for nonresonant stimuli; Table 2).

When the disk is held at 30 V, it produces an electric field of comparable magnitude to floral electric fields and can be detected by bees on the wing (14). For a fixed disk voltage, the electric field strength  $E$  varies with distance  $r$  from disk as  $E \propto r^{-2}$  (Fig. 4). The maximum distance at which the disk actuates the hair or antennae can then be used as a proxy for how relatively sensitive the structure is to an electric field. Accordingly, charged hairs can be actuated by a 30-V disk at a distance of 7.1–55 cm depending on stimulus frequency. Antennae are actuated at a maximum distance of 2.6–13 cm depending on stimulus frequency (Table 2 and Figs. 4 and 5). These distances of detection are consistent with the bumblebee's behavioral abilities reported by Clarke et al. (14).

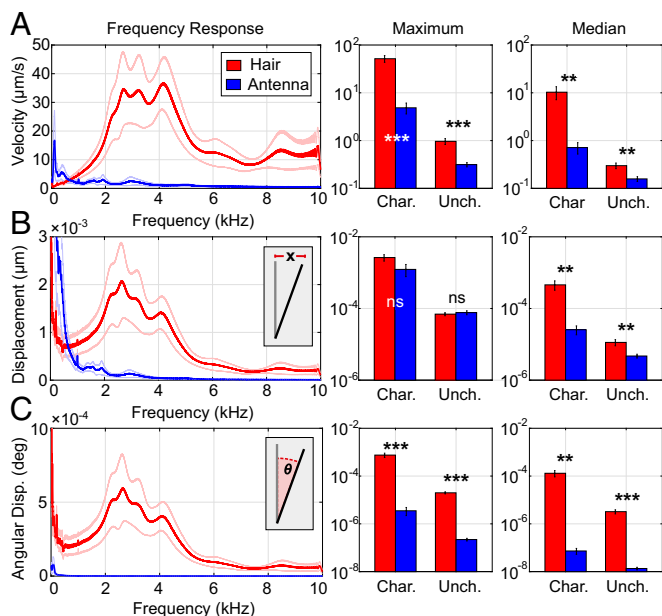
**The Effect of Electric Charge on Electromechanical Responses.** Bees accumulate charge during motion through their environment, (14, 17). A similar phenomenology likely applies to other flying or walking insects (18, 19). The bees used in this study, even in their charged state, carried less charge than they do in vivo [in vivo charge:  $32 \pm 3 \text{ pC}$  (15); experimental charge:  $4 \pm 1 \text{ pC}$ ,  $n = 10$ ]. Nevertheless, the effect of this small charge on the mechanical sensitivity of both hairs and antennae was pronounced. Charged bees respond with significantly greater amplitude than uncharged bees (paired  $t$  tests between charged and uncharged preparations  $P < 0.01$  throughout). This difference corresponds to a 5- to 53-fold increase in electromechanical sensitivity, across all measurements, between bumblebees carrying no charge and those carrying one-tenth of the charge of a free-flying bumblebee (Table 1).

**Electromechanical Responses of Hairs and Antennae to DC Electric Fields.** Hairs and antennae were stimulated with a 400-V square pulse lasting 1 s. The onset of the electric field produces a transient velocity signal measured by the laser that was integrated with

**Table 1.** Key results from laser Doppler vibrometry experiments

Quantity	Type	Charged		Uncharged			
		Hair	$P$	Antenna	Hair	$P$	Antenna
Velocity, $\mu\text{m/s}$	95 pctl	$51.8 \pm 8.3$	***	$4.9 \pm 1.2$	$0.97 \pm 0.1$	***	$0.31 \pm 0.03$
	Median	$10.3 \pm 3.1$	**	$0.71 \pm 0.19$	$0.30 \pm 0.04$	**	$0.16 \pm 0.02$
Disp., nm	95 pctl	$2.6 \pm 0.5$	n.s.	$1.2 \pm 0.5$	$0.070 \pm 0.01$	n.s.	$0.077 \pm 0.01$
	Median	$0.5 \pm 0.1$	**	$0.026 \pm 0.01$	$0.011 \pm 0.002$	**	$0.005 \pm 0.001$
Ang. disp, $\text{deg} \times 10^{-9}$	95 pctl	$13,200 \pm 270$	***	$61.7 \pm 23$	$345 \pm 34$	***	$3.84 \pm 0.49$
	Median	$2,290 \pm 670$	***	$1.28 \pm 0.4$	$56.6 \pm 11$	***	$0.24 \pm 0.03$

Shown are the 95th percentile (pctl) and median values of velocity, displacement (Disp.), and angular displacement (Ang. disp.) in response to 10 Hz–10 kHz sinusoidal electrical chirps at 400 Vpp amplitude. Results are from both charged and uncharged preparations. Asterisks show significance of difference between hair and antennae response under identical preparation and stimulation [ $t$  test (paired): \*\*\* $P \leq 0.01$ ; \*\* $P \leq 0.001$ ;  $n = 10$ ]. n.s., not significant.

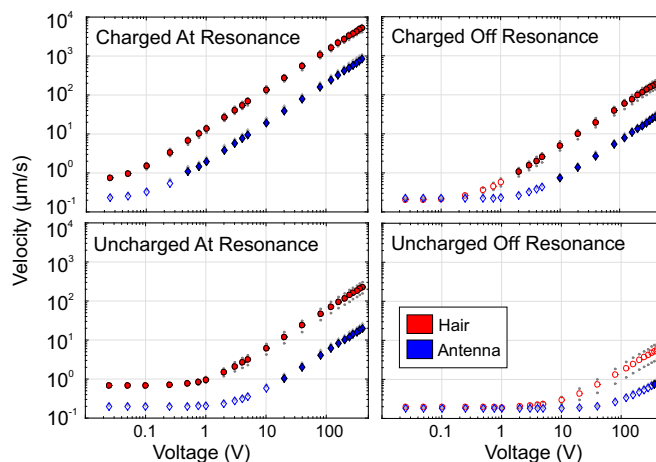


**Fig. 2.** Antenna (blue) and hair (red) motion in response to 10 Hz–10 kHz electrical chirps. Rows show the velocity (A), displacement (B), and angular displacement (C). Columns show the response at each frequency (Left), the amplitude of maximum response (Middle), and the median response amplitude across all frequencies (Right). Insets show a representation of the quantity being measured.

respect to time to give the change in position of the structure. This experiment was only performed on charged bees. The average displacement for antennae was  $1.2 \pm 0.4 \mu\text{m}$ . This displacement is consistent with observations of the antennae in honeybees, which are displaced  $\sim 1 \mu\text{m}$  in response to 450 V, 40 Hz electric stimuli (15). The average displacement of the hairs was significantly lower at  $0.14 \pm 0.05 \mu\text{m}$  (paired *t* test:  $P < 0.005$ ). The corresponding angular displacements were  $(3.3 \pm 1) \times 10^{-3}$  degrees for the antennae and  $(3.7 \pm 0.01) \times 10^{-2}$  degrees for the hairs. In response to the same static electric field, the angular deflection of the hair was 11 times greater than the angular deflection of the antenna (paired *t* test:  $P < 0.001$ ,  $n = 10$ ). If 400 V is applied to a needle, which concentrates the electric field near the tip, the hair can be moved hundreds of micrometers, a motion large enough to be visible under the microscope (Movie S1).

**Bumblebee Hairs Exhibit Neural Correlates to DC Electric Field Stimulation.** To determine whether the observed mechanical deflection is accompanied by a response from the nervous system, we measured the electrophysiological response of hairs and antennae to a 400-V square pulse applied to a steel disk 1 cm away (Fig. 6A–C). All electrophysiological recordings were carried out on bees in their uncharged state, due to the necessity of grounding the bee to eliminate noise from the recording.

Bumblebee hairs ( $n = 12$ ) showed an increase in neural firing rate in response to the applied DC electric field (Fig. 6B and C). Some hairs had a background firing rate, whereas others were quiet before stimulus application. During the stimulus, the mean firing frequency of hairs was 5.1 times greater than the prestimulus firing rate (paired *t* test:  $P < 10^{-6}$ ,  $n = 14$ ). In contrast, stimulation failed to increase firing frequency in the antennae (paired *t* test:  $P > 0.05$ ,  $n = 14$ ) (Fig. 6C). Dynamic stimulation at 140 Hz ( $n = 5$ ) also failed to elicit an electrophysiological response from the antenna (SI Methods and Materials). In control recordings (Fig. 6E and SI Methods and Materials), however, the antenna responded to mechanical (air puffs) and olfactory (lavender oil) stimuli, showing



**Fig. 3.** Antenna (blue) and hair (red) mean velocity in response to oscillating electric fields at the resonant frequency of each structure (Left) and at the frequency of median response (Right) under charged (Top) and uncharged (Bottom) preparations. Gray dots show SEM. Filled shapes denote responses that were significantly larger than thermal noise. Unfilled shapes denote responses statistically indistinguishable from thermal noise.

the adequacy of the present electrophysiological preparation. These responses were consistent with previously reported antennal sensitivity to mechanical and olfactory stimulation (20).

## Discussion

From this evidence, we conclude that bumblebees use mechano-sensitive hairs to detect electric fields. In honeybees (*Apis mellifera*), the antenna has been proposed to detect electric fields, whereby Johnston's organ transduces mechanical deflections of the flagellum in response to an electric field analogous to that generated during a honeybee's waggle dance (15). Cockroach antennae have been shown to react to more intense electric fields, in the range of  $8\text{--}10 \text{ kV}\cdot\text{m}^{-1}$  (21). Our similar experiments in bumblebees failed to demonstrate that antennae could respond to electric fields.

Mechanosensory hairs are common across the Phylum Arthropoda (16). These sensors typically have mechanical resonances between 100 and 500 Hz and react to vibrations from the wingbeats of approaching predators (22) and air currents (23, 24). In contrast, bumblebee hairs have a resonant frequency of approximately 3.8 kHz, a result of low mass and high stiffness. Their rigid lever-like motion within the socket resembles the acoustic particle velocity induced response of other mechanically sensitive hairs (25) and the feathery antennae of mosquitoes (26). Bumblebee hairs neurally respond to electrically induced deflections of  $4 \times 10^{-2}$  degrees (Table 1), making them less sensitive than cricket filiform hairs,

**Table 2.** The minimum voltage on a disk 1 cm away from a bumblebee required to produce a mechanical response ( $U_{\text{min}}$ ), the electric field corresponding to this voltage ( $E_{\text{min}}$ ), and the axial distance from a 30-V disk at which electric field strength is equal to this value ( $D_{\text{max}}$ )

Quantity	Charged		Uncharged	
	Hair	Antenna	Hair	Antenna
$V_{\text{min}}$ at resonance, V	0.025	0.5	0.025	20
$V_{\text{min}}$ off resonance, V	2	10	400	360
$E_{\text{min}}$ at resonance, $\text{V}\cdot\text{m}^{-1}$	0.77	15	0.77	612
$E_{\text{min}}$ off resonance, $\text{m}^{-1}$	61	306	12,249	11,024
$D_{\text{max}}$ at resonance, cm	55	13	55	1.6
$D_{\text{max}}$ off resonance, cm	7.1	2.6	0.1	0.6





study enables the formulation of the tantalizing hypothesis that, through the electromechanical sensitivity of hairs, electroreception is widespread in arthropods, fulfilling functions beyond the detection of floral electric fields.

## Methods and Materials

### Laser Vibrometry.

**Bee preparation.** Bees were killed with CO<sub>2</sub> and glued ventrally with cyanoacrylate to an electrically isolated piece of wood. They were attached to a mounting pin and placed in front of a laser Doppler vibrometer for measurement of antennal and hair vibration velocity (Fig. 1B). The bee was electrically charged by contact with a frictionally charged nylon ball bearing and left to settle for 10 min. After undergoing charging, bees carried an average of  $4 \pm 3$  pC, where uncharged bees carried  $0 \pm 0.5$  pC. The charge carried by a bumblebee *in vivo* is  $32 \pm 3$  pC (14), hence in the experiments the charging below that measured in free flight. Charge stimuli used here are thus within the range of naturally occurring electrostatics. After initial measurements, the bee's charge was neutralized by application of a positive and negative ion beam (*SI Methods and Materials*). The stimulus regime was then repeated.

**Vibrometry.** Measurements of mechanical response of hairs and antennae to electric field stimuli were taken with a microscanning LDV (Polytec PSV300) fitted with a close-up attachment. Data were acquired by using an OFV5000 sensor head, digitized via an on-board data acquisition card (National Instruments PCI-4451) and subsequently analyzed by using PSV software (Polytec version 9.0). The target, laser source, and stimulus delivery disk are placed on the same horizontal plane on an antivibration table (TMC 784-443-12R) in an electrically isolated and sound-proofed booth (*SI Methods and Materials* and Fig. 1C).

**Stimulus regime.** Electrical stimuli were delivered by using an arbitrary function generator (Agilent 33120A) connected in series to a custommade high voltage amplifier. The stimulation electric field was generated by a 30-mm-diameter steel disk connected to the high voltage amplifier by an earthed 50 Ohm BNC cable (as in ref. 14). A 400-V periodic sweep from 10 Hz to 10 kHz was applied

to the disk. The frequency response and resonant frequency were recorded. To test for response amplitude relationship, a pure tone sine wave set at the resonant frequency was applied and the hair/antenna response recorded for incrementally decreasing stimulus amplitudes (400-380-360...-0 V). Stimulus amplitude was then increased back up to 400 V to test each result for linearity. This stimulus was repeated for a second, off-resonant frequency that was chosen by identifying a frequency at which the amplitude of the response was equal to the median response amplitude across all frequencies. The bee was then prepared in its uncharged state, and the whole regime was repeated. This entire procedure was repeated for both hairs and antennae.

**Electrophysiology.** Anesthetized bees were ventrally affixed to a post made of modeling clay (*SI Methods and Materials*). Extracellular recordings were made from both the antenna and the hair using electrolytically sharpened tungsten electrodes (*SI Methods and Materials*), using a National Instruments data acquisition card (NI 9172/9215) and custom-built amplifier and LabVIEW 2011 to record the signal. For antennal recordings, the experimental electrode was inserted at the proximal end of the scape. The reference electrode was placed in the head, taking care not to place it near an ommatidium. For hair recordings, the experimental electrode was inserted in the basal socket. The reference electrode was placed in nearby cuticle.

Stimuli were delivered with the disk placed 1.0 cm from the bee in an identical arrangement to the LDV experiments. For all trials, there was an initial 10 s of no stimulation, followed by 10 s of electrical stimulation at 400 V, followed by 10 s of no stimulation. For the antennae, additional control stimuli in the form of air puffs, scent, and AC electric fields were applied (*SI Methods and Materials*).

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