COMMENTARY

Electric fields of flowers stimulate the sensory hairs of bumble bees

Harold H. Zakon[a,b,1]

Most of us have been shocked after walking across a carpet and touching a metal doorknob. The build-up of charge—"static" electricity—on the surface of some nonconductors because of friction is called triboelectricity. We are unaware of the build-up of charge on our bodies as we walk and only notice it upon discharge when it briefly stimulates our pain-sensing neurons; it is essentially an epiphenomenon for us. That positive charge builds up on flying insects, such as bees, has been appreciated for decades (1, 2). Similarly, flowers hold electric charge and their negatively charged pollens are attracted to the positive charge on the bodies of alighting bees (3). So at the very least, a bee's accumulation of charge is harnessed to aid in pollination. But, do bees sense the charge on their bodies or on flowers, and use this information to guide their behavior or, like us, are they unaware of it? If bees sense electric fields, then how? A recent set of experiments by Robert and colleagues demonstrated that bumble bees (*Bombus terrestris*) indeed sense a flower's electric fields, that these convey important information to them (4) and, in an article in PNAS (5), Sutton et al. show that these electric fields are sensed by electrostatic movements of the many mechanosensory filiform hairs over their bodies.

In their first study, Clarke et al. (4) showed that flowers have distinct patterns of electric charge over their surface, and that bees learn to discriminate charged and uncharged artificial flowers. Adding electric patterns to visual patterns on these flowers enhanced the bees' rate of discrimination learning. One other interesting point is that when bumble bees land on flowers, some of the positive charge from their bodies moves to the flower and cancels some of the flower's negative charge; this lasts for 1 to 2 min (Fig. 1). The authors hypothesized that a bee might use the net charge of a flower to judge if the flower has been recently visited by another bee and, therefore, has diminished offerings of nectar and pollen.

In PNAS, Sutton et al. (5) test the sensitivity of two candidate structures for sensing electric charge: the many tiny filiform hairs distributed over the head and body, and the antennae, both of which are deflected

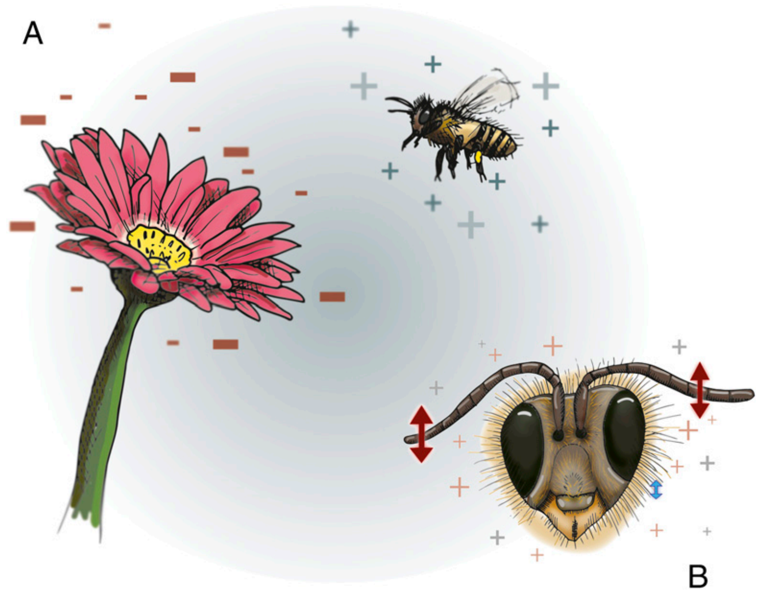

Fig. 1. A bumble bee can detect the electric fields of flowers via the deflections of many tiny mechanosensory filiform hairs on its head and body. (*A*) Bees accumulate positive charge on their bodies as they fly. Flowers have negative charges. The interaction of these charges when a bumble bee alights on a flower mechanically moves the bee's antennae and filiform hairs. (*B*) Stimulation of antennae or filiform sensory hairs with electric charge moves them. The electro-mechanical movements of the bumble bee antenna (red arrows) do not activate antennal sensory neurons, whereas movements of the filiform hairs (blue arrows) do.

by electric charge and innervated. The hypothesis is that the movement of either or both structures by an electric charge is detectable by the mechanosensory neurons that innervate the filiform hairs and the base of the antenna. In other words, there is no dedicated electroreceptor per se, as found in sharks or electric fish (6, 7), but rather the electrically forced movement of a mechanosensory structure. Using laser Doppler vibrometer, Sutton et al. (5) measured the movements of these structures to applied electric fields, finding that the filiform hairs move with an order-of-magnitude greater velocity than the antennae to the same applied fields. The key experiment was recording from the mechanosensory neurons emanating from the

[a]Department of Neuroscience, The University of Texas at Austin, Austin, TX 78712; and [b]Department of Integrative Biology, The University of Texas at Austin, Austin, TX 78712

Author contributions: H.H.Z. wrote the paper.

The author declares no conflict of interest.

See companion article 10.1073/pnas.1601624113.

[1]Email: h.zakon@austin.utexas.edu.

base of antennae and the filiform hairs to the application of ecologically relevant electric fields. Despite the movement of the antennae by applied voltages, the antennal neurons did not respond, whereas those from the filiform hairs responded robustly. As a control, the authors show that antennal neurons responded to mechanical deflections or olfactory stimuli.

These results differ from other recent studies that emphasized the role of antennal mechanosensors of honey bees (*Apis mellifera*) (8) and cockroaches (9) in responding to electric charge. Greggers et al. (8) found that, in addition to the list of known sensory stimuli used by honey bees to communicate their movements to hive mates during the waggle-dance (10), they sense the modulations of the amplitude of the electric fields on their bodies as they move their abdomens and wings closer to or away from neighboring bees. Greggers et al. (8) showed that the antennae move in response to these modulations, and they recorded strong neural responses from the mechanosensors in the antennae to these electric fields. The authors did not test, and therefore do not rule out, the involvement of other mechanoreceptors, such as filiform hairs. Although the differences between bumble bees and honey bees may yet be true species differences or might result from slight differences in experimental design, the bigger take-home message of all of these studies is that insects have a triboelectric sense mediated by mechanoreceptors.

These papers pry open the lid on what is likely to be a rich trove of future experimental questions. Because the same neurons seem to convey both mechanosensory and electric cues, can these cues be independently discriminated? What does the brain do with this information: are there distinct mechanosensory and electrosensory channels? Because it seems likely that the mechanosensory hairs are stimulated by wind and the bee's own wing-flapping as a bee approaches a flower, how does this interact with the detection of electric stimuli?

Bumble bees and some other insect pollinators (but apparently not honey bees) increase their pollen yield by "buzz" pollination, whereby they anchor themselves on the bottom of the flower's anther with their mandibles and shake it at 100–400 Hz, with their thoracic muscles causing the anther to release a shower of pollen (11). Does this close coupling between plant and bee and the frenetic activity of the bee dissipate or build charge and facilitate or degrade the bee's interaction with the next flower or the flower's interaction with the next bee?

Is there a triboeletric sense in other insects? If accumulation of charge on an insect's body is as widespread as appears likely (9), is it an epiphenomenon or even a nuisance in some species—perhaps even suppressed centrally as noise—but used in others? Have other insect pollinators—such as wasps, moths, butterflies, flies, and beetles—also evolved to interact electrically with their flowers? It has been known for over 100 y that charge is held on the hair of mammals and feathers of birds (12). Similar to bees, pollen may be electrostatically attracted to approaching hummingbirds (13). Might hummingbirds and other nectarivorous pollinating birds, or perhaps some pollinating mammals such as bats, have evolved a similar triboelectric sense?

Finally, there is a potential downside to living in a world where triboelectricity exerts a real force; spider webs sometimes accumulate negative charge and are pulled toward, and snag, nearby positively charged insects (14). So, the force may be with them—or against them.

Acknowledgments

The author acknowledges Ms. Nicole Elmer for creating Fig. 1.

1 Heuschmann O (1929) Über die elektrischen Eigenschaften der Insekten Haare. *Z Vgl Physiol* 10(4):594–664.
2 Edwards DK (1962) Electrostatic charges on insects due to contact with different substrates. *Can J Zool* 40(4):579–584.
3 Corbet SA, Beament J, Eisikowitch D (1982) Are electrostatic forces involved in pollen transfer? *Plant Cell Environ* 5(2):125–129.
4 Clarke D, Whitney H, Sutton G, Robert D (2013) Detection and learning of floral electric fields by bumblebees. *Science* 340(6128):66–69.
5 Sutton GP, Clarke D, Morley EL, Robert D (2016) Mechanosensory hairs in bumblebees (*Bombus terrestris*) detect weak electric fields. *Proc Natl Acad Sci USA*, 10.1073/pnas.1601624113.
6 Kalmijn AJ (1971) The electric sense of sharks and rays. *J Exp Biol* 55(2):371–383.
7 Zakon H (1986) The electroreceptive periphery. *Electroreception*, eds Bullock T, Heiligenberg W (Wiley, New York), pp 103–156.
8 Greggers U, et al. (2013) Reception and learning of electric fields in bees. *Proc Biol Sci* 280(1759):20130528.
9 Newland PL, et al. (2008) Static electric field detection and behavioural avoidance in cockroaches. *J Exp Biol* 211(Pt 23):3682–3690.
10 Dyer FC (2002) The biology of the dance language. *Annu Rev Entomol* 47(1):917–949.
11 De Luca PA, Vallejo-Marín M (2013) What's the 'buzz' about? The ecology and evolutionary significance of buzz-pollination. *Curr Opin Plant Biol* 16(4):429–435.
12 Exner S (1895) Über die Elektrischen Eigenschaften der Haare und Federn. *Pflugers Arch* 61:1–98.
13 Badger M, Ortega-Jimenez VM, von Rabenau L, Smiley A, Dudley R (2015) Electrostatic charge on flying hummingbirds and its potential role in pollination. *PLoS One* 10(9):e0138003.
14 Ortega-Jimenez VM, Dudley R (2013) Spiderweb deformation induced by electrostatically charged insects. *Sci Rep* 3:2108.