

Detection and Learning of Floral Electric Fields by Bumblebees

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Insects use several senses to forage, detecting floral cues such as color, shape, pattern and volatiles. We report a formerly unappreciated sensory modality in bumblebees (*Bombus terrestris*), detection of floral electric fields. These fields act as floral cues, which are affected by the visit of naturally charged bees. Like visual cues, floral electric fields exhibit variations in pattern and structure, which can be discriminated by bumblebees. We also show that such electric field information contributes to the complex array of floral cues that together improve a pollinator's memory of floral rewards. Because floral electric fields can change within seconds, this sensory modality may facilitate rapid and dynamic communication between flowers and their pollinators.

Flowers produce a diverse range of cues and attractants to pollinators and in doing so act as sensory billboards (1). The diversity of floral cues encompasses intricate color hues and patterns, petal texture, fragrant volatiles, local air humidity and echolocation fingerprints (1–4). The impact of floral cues on pollinator behavior has been observed since Aristotle (5), yet new floral cues are still being discovered (3, 4). Multimodal floral cues have been found to enhance both pollinator foraging efficiency and pollination (6), and thus facilitate increased seed and fruit set.

Flying insects, including pollinators like honeybees, usually possess a positive electric potential (7–10). Conversely, flowers often exhibit a negative potential (7, 11). Electric fields arising due to this potential difference between flowers and insects promote pollen transfer and adhesion over short distances (7, 8, 12, 13). Furthermore, these fields differ according to the pollination status of the flower as the deposition of pollen and resulting pollination changes flower electric potential (14, 15). However, the use of electric fields by pollinators as informative cues has not been investigated. In the complex world of plant-pollinator interactions, any cue that increases pollination and foraging efficiency should be mutually beneficial. Here, we report that bumblebees can detect and learn to use floral electric fields, and their structural variation, to assess floral reward and discriminate among flowers.

The electrical interactions between the bee and the flower arise from the charge carried by the bee and the potential of the flower in relation to the atmospheric electric field. To quantify bee charge, individual *B. terrestris* workers were trained to fly into a Faraday pail that contained a sucrose reward. The net charge q carried by the bee was measured from the induced voltage on a calibrated capacitor (methodology described in Supplementary Online Materials). Measured on 51 individuals, 94% of bees were positively charged and 6% negatively charged ($q_{\text{mean}}=32 \pm 5\text{pC}$, $SD=35\text{pC}$) (Fig. 1A). These results corroborate previous measurements on the honeybee *Apis mellifera* (9), and establish that the majority of bees flying in the arena carry a positive charge susceptible to transfer.

Electrical interaction between bee and flower was further explored by placing *Petunia integrifolia* flowers in an arena with free-flying foraging bees. The electric potential in *Petunia* stems was recorded to assess the electrical signature produced by the approach and landing of an individual charged bee. Charge transfer to the flower resulted in a posi-

tive change in electric potential recorded in the stem. The landing of 50 individuals resulted in a mean potential change lasting ca. 100s, which peaked at ca. $25 \pm 3\text{mV}$ ($SD=24$, $n=50$) (Fig. 1B). Such change exceeds natural fluctuations in the absence of bees (Fig. 1B) and outlasts the presence of the bee on the flower. This change in potential is often initiated prior to contact with the bee (video S1), suggesting that this is not simply a hydraulic wound-response variation potential as in (16) but involves direct electrostatic induction between the charged bee and the grounded flower as hypothesized in (7, 8).

Because the floral electric potential is directly affected by pollination (14, 15) and bee visitation (Fig. 1B), it potentially carries information for other visiting pollinators regarding floral resources. Visiting pollinators impact on floral cues directly, by leaving scent marks on the petal surface, or by initiating

changes in floral cues, such as color, shape and humidity (4, 17–19). Such changes typically occur in the timeframe of minutes to hours. The variation potential produced by bee visitation occurs within a timeframe of seconds (Fig. 1B).

For a floral electric field to act as a cue, it must be possible for pollinators to detect and discriminate it from the background. We used differential conditioning (3) to test the ability of bumblebees to discriminate between artificial flowers (E-flowers) with differing electric fields. E-flowers consisted of a 35mm diameter \times 1.5mm thick steel base disk decorated with a purple epoxy top disk. Half the E-flowers were held at a biologically relevant 30V DC bias voltage. This voltage was chosen as a proxy for the electric field of an isolated flower standing 30cm tall in a typical 100Vm^{-1} atmospheric electric field (Fig. 3B) (20). Charged E-flowers offered a sucrose reward, while identical E-flowers were held at ground (0V) and provided a bitter quinine hemisulphate solution (3). E-flowers were indistinguishable in every other respect. During the course of 50 bee visits, there was an increase in the relative number of visits to rewarding charged flowers (Fig. 2A). To measure bee learning, we compared the mean accuracy of the final ten visits (visit 41–50) to a random choice model. In their final ten visits to 30V charged E-flowers, bees ($n=11$) achieved $81 \pm 3\%$ accuracy ($T_{1\text{-sample}}=10.8$ $p=7.4 \times 10^{-7}$). Both flower types were then grounded and the choice test continued. Without the electric cue, the same set of trained bees was no longer able to discriminate between the rewarding and unrewarding E-flowers, also demonstrating the absence of systematic experimental bias. Accuracy after the electric cue is removed was $54 \pm 4\%$, which does not differ significantly from random choice ($T_{1\text{-sample}}=1$ $p=0.35$) (Fig. 1B). Using a 10V bias failed to elicit significant learning ($n=10$ mean accuracy = $56 \pm 4\%$ $T_{1\text{-sample}}=1.4$ $p=0.19$) (Fig. 2A, B).

Floral cues are diverse and address the multimodal perception of pollinators. Working in concert, floral cues enhance foraging efficiency (6), and constitute a complex informational ecology of competing flower advertisement. Color cues rely both on hue and on contrast between hues and their geometrical patterns. Nectar guides constitute such patterns, providing information attractive to pollinators and facilitating foraging efforts (21,22). By analogy, the geometry of floral electric fields may carry additional information important for pollinators. The diversity of floral electric field geometry can be experimentally visualized by coating

flowers with positively charged colored particles released as an aerosol close to the corolla. The heterogeneous pattern of color deposition reveals the structure of the electric field at the flower's surface (Fig. 3A).

Electric field structure was also visualized using finite element (FE) modelling of an idealized 30 cm tall flower in a physically realistic, 100V m^{-1} atmospheric electric field (20) (Fig. 3B, left panel). Plants are conductively linked to ground via their stems and roots, a connection that maintains them close to ground potential (7). Hence, a grounded 30cm tall plant in such an atmospheric electric field exhibits a 30V potential difference between its inflorescent structures and the surrounding air, exhibiting a patterned electric field (Fig. 3B). This experimental and modelling evidence reveals that flower morphology determines electric field geometry.

To test the bee's ability to discriminate E-field geometries, differential conditioning was used with two types of E-flowers, providing similar voltage but different local patterns (Fig. 3C). Rewarding E-flowers presented a bull's eye pattern, with the outer ring held at +20V and the center ring at -10V. Aversive E-flowers presented a homogenous voltage at +20V (Fig. 3C). Bees ($n=10$) learned to discriminate between these two patterns, reaching $70 \pm 3\%$ accuracy over their final 10 visits, performing significantly better than random choice ($T_{1\text{-sample}}=6.7$ $p=8 \times 10^{-5}$) (Fig. 3E). After this task, a subset of the bees ($n=4$) was allowed to complete 50 additional visits to rewarding and aversive E-flowers with identical homogenous +20V fields. These bees failed to discriminate between E-flowers (Fig. 3E). Altogether, these tests show that bumblebees can discriminate charged from uncharged flowers, and can distinguish between flowers that differ in the geometry of their electric field. As such, E-fields could be used by flowers to provide information to their pollinators.

Floral cues can work individually or complementarily (1, 6). When presented together, multimodal cues enhance the certainty of sensory information used by honeybees. Specifically, the association of color with olfactory floral cues reduces the bees' perceptual uncertainty related to an individual floral cue and increases their ability to distinguish between rewarded and aversive stimuli (23). The hypothesis can be formulated that the floral electric field reinforces the effectiveness of other floral cues. If true, an electric cue paired with a color cue should produce an enhanced learning outcome equivalent to the test using color and scent. Differential conditioning was used to test this hypothesis. The same two green target hues were used as in (23), but olfactory cues were replaced with a patterned electric field (Fig. 3C). Bees were trained to discriminate between E-flowers of hue 120° HSB which offered a sucrose reward and E-flowers of hue 140° HSB providing an aversive quinine solution (Fig. 4A). Bees learned to discriminate between the rewarding and aversive charge-less E-flowers either using color information alone ($n=16$) or in combination with the patterned E-field ($n=18$) (Fig. 4A). When learning color on its own, discrimination to 80% success (i.e., 8 out of the last 10 choices correct) took 35 ± 3 visits. When combined with the E-field pattern, the number of visits required was significantly reduced to 24 ± 3 ($T_{2\text{-sample}; \text{unequal}}=2.86$ $p=0.008$) (Fig. 4A). This demonstrates that the combination of two cues, E-field and hue, enhances the bee's ability to discriminate.

We have discovered that electric field constitutes a floral cue. Contributing to a varied floral display aimed at pollinator senses, electric fields act to improve both speed and accuracy with which bees learn and discriminate rewarding resources. As such, electric field sensing constitutes a potentially important sensory modality, which now should be considered alongside vision and olfaction. The ubiquity of electric fields in nature and their integration into the bees' sensory ecology suggest that E-fields play a thus far unappreciated role in plant-insect interactions. The present study raises the possibility of reciprocal information transfer between plants and pollinators at time scales of milliseconds to seconds, much faster than previously described alterations in floral scent, color or

humidity (4, 18, 19). The remarkably accurate discrimination and learning of color patterns by bees was revealed by both laboratory and field training experiments (19, 21–23). Similarly, the present laboratory study reveals that floral electric fields occur in patterns and that they can be perceived. As such, our study provides a framework for exploration of the function and adaptive value of the perception of weak electric fields by bees in nature.

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Supplementary Materials

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Materials and Methods

References (24–26)

Movie S1

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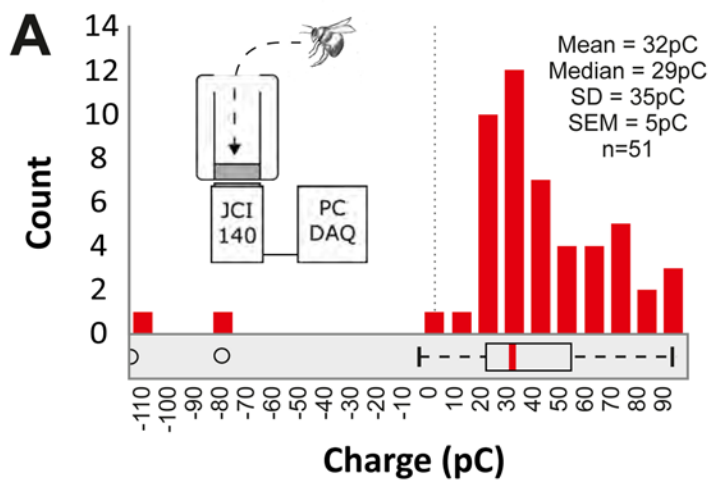
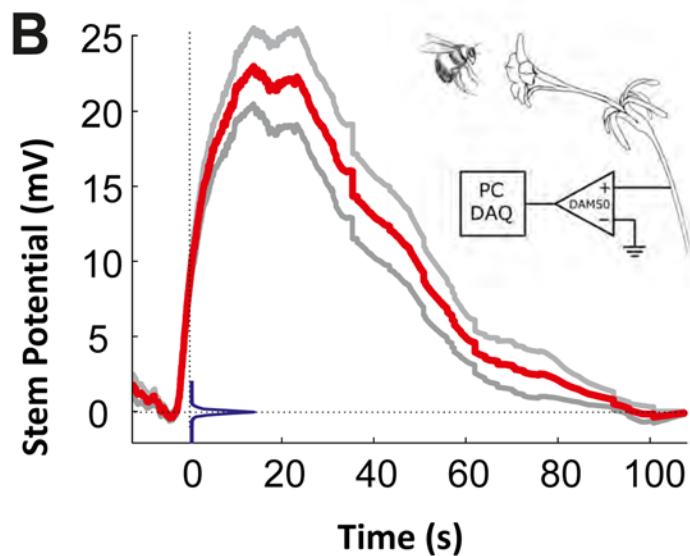


Fig. 1. Electric charge carried by bumblebees and its transfer to flowers. (A) Histogram of electric charge of flying bumblebees. Boxplot shows median, SD, interquartile range and outliers. (B) Mean variation potential in the *Petunia* stem resulting from bee landings (red, N=51), shown with ± 1 SEM (gray). Distribution of the natural variation of stem potential (measured along 35 samples of 30 s) in absence of bees, truncated at 2SD (blue).



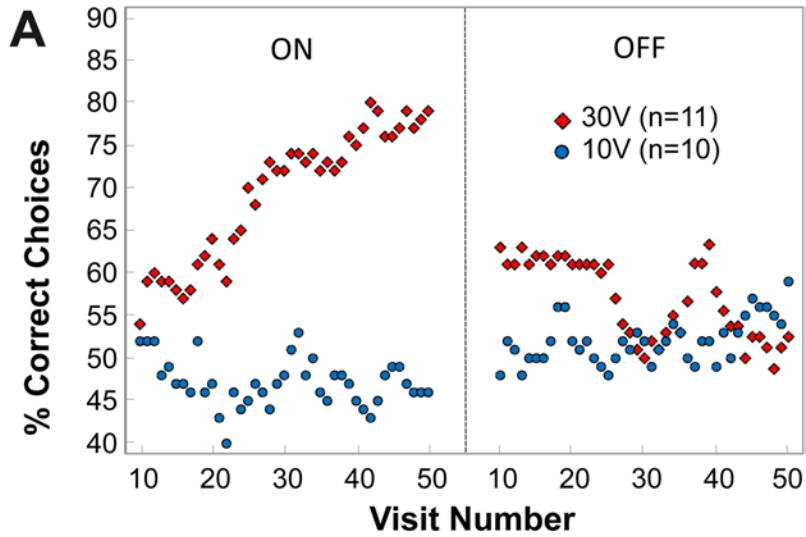
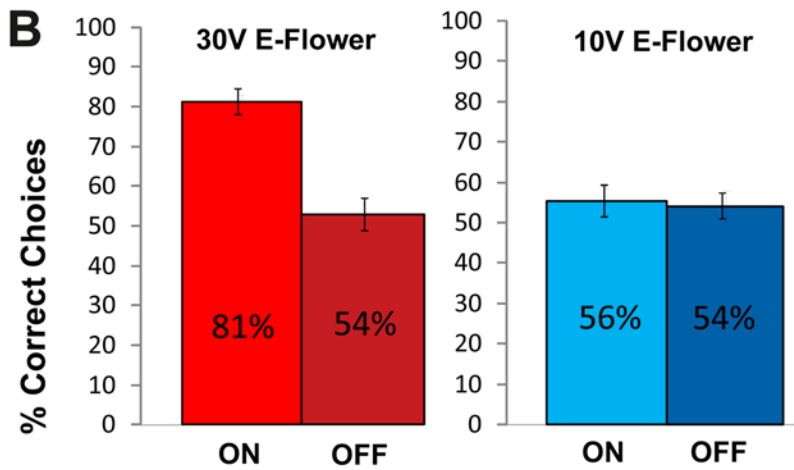


Fig. 2. Bumblebees learn the presence of an electric field. (A) Learning curves of foraging bees, trained to 30 (red diamonds) or 10V (blue circles) E-Flowers. Dashed line shows switching off electric field. (B) Mean correct choices to 30V (left) and 10V (right) E-Flowers over visits 41 to 50 in (A) during training (voltage on) and control (voltage off). Error bars show SEM.



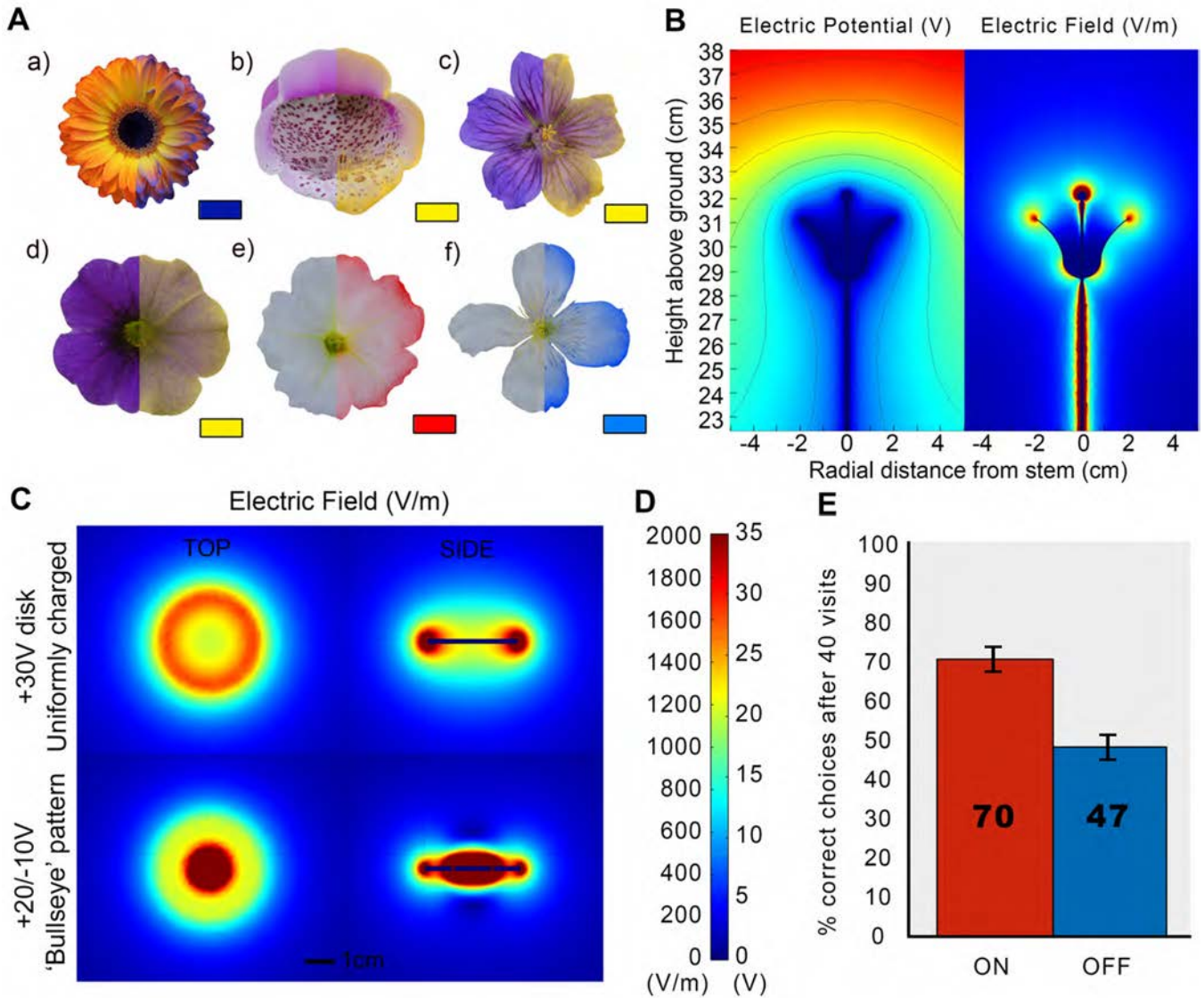


Fig. 3. Geometry of floral electric field and discrimination task. (A) Flowers before (left half) and after (right) spraying with electrostatic colored powder; a) *Gerbera hybrida* b) *Digitalis purpurea* c) *Geranium magnificum* d) *Calibrachoa hybrida* e) *Petunia hybrida* f) *Clematis armandii*. Density of powder deposition reflects the variation in electric field strength at the flowers' surface. (B) FE model of an idealized 30cm tall flower, equipotential with ground, in an atmospheric field of 100V/m. Left: scalar electric potential. Right: electric field magnitude. (C) FE models of electric field produced by E-flowers. (D) Scale for B and C. (E) Pattern discrimination as mean percent of correct choices over the last ten visits for patterns on and off. Error bars show SEM.

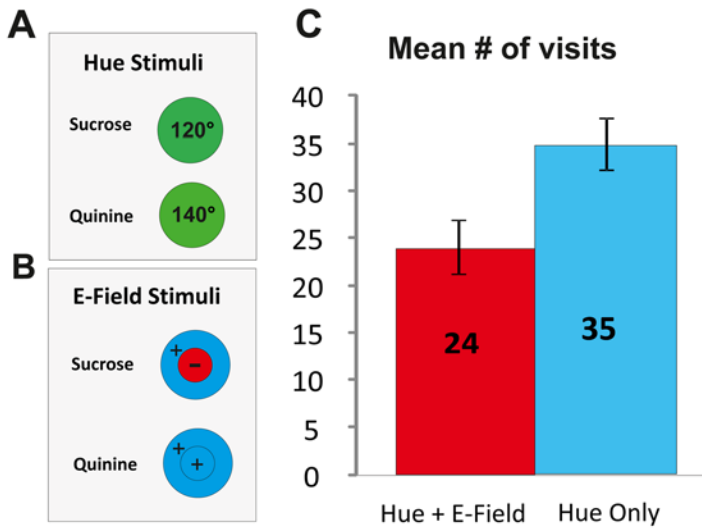


Fig. 4. Multimodal facilitation. Colors (A) and voltage configurations (B) associated with rewarding and aversive E-flowers. (C) Mean number of visits taken by bees in each group to reach 80% correct choices.