

Conical Epidermal Cells Allow Bees to Grip Flowers and Increase Foraging Efficiency

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Summary

The plant surface is by default flat, and development away from this default is thought to have some function of evolutionary advantage. Although the functions of many plant epidermal cells have been described, the function of conical epidermal cells, a defining feature of petals in the majority of insect-pollinated flowers, has not [1, 2]. The location and frequency of conical cells have led to speculation that they play a role in attracting animal pollinators [1, 3, 4]. Snapdragon (*Antirrhinum*) mutants lacking conical cells have been shown to be discriminated against by foraging bumblebees [4]. Here we investigated the extent to which a difference in petal surface structure influences pollinator behavior through touch-based discrimination. To isolate touch-based responses, we used both biomimetic replicas of petal surfaces and isogenic *Antirrhinum* lines differing only in petal epidermal cell shape. We show that foraging bumblebees are able to discriminate between different surfaces via tactile cues alone. We find that bumblebees use color cues to discriminate against flowers that lack conical cells—but only when flower surfaces are presented at steep angles, making them difficult to manipulate. This facilitation of physical handling is a likely explanation for the prevalence of conical epidermal petal cells in most flowering plants.

Results and Discussion

The coevolution between flowering plants and their animal pollinators has resulted in a wide diversity of floral forms, whereby angiosperm flowers display arrays of features thought to increase floral attractiveness and memorability to flower visitors. Foraging pollinators therefore learn a variety

of different cues when visiting a flower, including color, scent, floral shape, and patterning [5–15]. Previous studies have shown that detectable cues will be discriminated for by pollinators if their presence facilitates foraging [15]. The epidermal surface of the petals of most flowering plants is composed of cone-shaped (conical) cells (Figure 1). In one study that examined 201 species from 60 families, 79% were found to exhibit some form of conical cells on the adaxial petal epidermis [1]. Can differences in floral surface texture such as the presence of conical cells act as one of these abovementioned detectable cues, and is this explanation sufficient to explain their frequency among flowering plants?

No Volatile Differences between *Antirrhinum* Mutant Lines Differing in Petal Cell Shape

We have explored the possible adaptive benefit of petal surface structure, and disentangled it from other floral traits, via mutant lines that differ in epidermal cell shape. The *mixta* line of *Antirrhinum* was initially isolated because of its color, a paler pink than the rich magenta of the wild-type flower [16]. This reduction in color saturation was found to be due to a change in cell shape on the petal surface and the consequent reflection of increased amounts of white light [17]. Because of a mutation at the *MIXTA* locus, the cells of the inner epidermis of the corolla are prevented from developing the conical form of the wild-type, resulting in a flat shape (Figure 1). The *MIXTA* gene encodes a MYB transcription factor expressed solely in the epidermal petal cells and thus has no pleiotropic effects [16, 18]. However, it has been suggested that altering the surface area of the epidermal cells, the location of floral volatile synthesis in many flowers, could potentially alter the volatiles produced in these lines [19]. Although the differences in the ratio of volatiles emitted can be of crucial importance in honeybee discrimination responses to different *Antirrhinum* cultivars [8], our data confirm that bees in earlier field trials and in our flight arena would not have been able to make use of any olfactory cue. There is no significant difference between the scent produced by the wild-type (magenta conical-celled, genotype *Mixta/Nivea*) and the *mixta* mutant (magenta flat-celled, genotype *mixta/Nivea*) lines used in this study, or between their white-flowered counterparts the *nivea* mutant (white conical-celled, genotype *Mixta/nivea*) and the *mixta/nivea* double mutant (white flat-celled), when volatiles were collected via headspace analysis. Gas chromatography and gas chromatography-mass spectrometry confirmed that the same volatiles were produced by all flower types, in the same proportions (see Figure S1 available online), eliminating olfactory cues and leaving only the tactile difference between petals as a learnable cue.

Tactile Discrimination of Floral Surface Textures by Foraging Bumblebees

Previous work has described the remarkable discovery that honeybees can learn to identify flowers by touch when neither visual nor olfactory cues are available [3, 20, 21]. The surface structures on floral petals are exceedingly fine-grained: conical cells have a diameter across the base in the range of 10 μm, and it is thought that bees discriminate these structures

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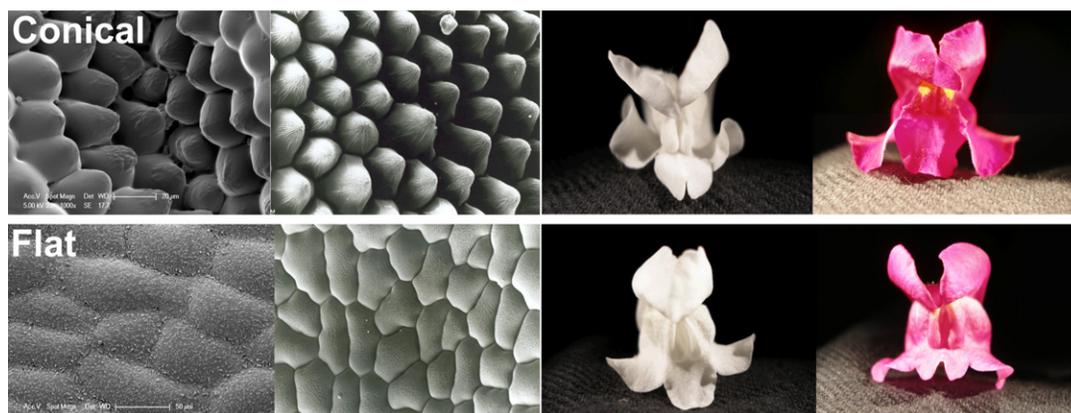


Figure 1. Conical-Celled and Flat-Celled Petal Surfaces and Flowers

Top row, left to right: scanning electron microscopy of epoxy cast of rose flowers, scanning electron microscopy of wild-type *Antirrhinum*, conical-celled *nivea* flower, conical-celled wild-type flower. Bottom row, left to right: scanning electron microscopy of epoxy cast of magnolia flower, scanning electron microscopy of *mixta* mutant *Antirrhinum* petal, flat-celled *mixta/nivea* double-mutant flower, flat-celled *mixta* flower. Scale bars represent 20 μm .

with the sensilla trichodea on the tips of the antennae [3]. However, these earlier studies used dried flowers and included flower surfaces that differed in both the micro- and macro-structure, in that the flowers used were from different families. In our experiments, we used the isogenic *nivea* (white with conical cells) and *mixta/nivea* (white with flat cells) lines of *Antirrhinum*. These are indistinguishable to both the human eye and the insect eye [18, 22]. Differential conditioning was used [23], with a bitter quinine solution presented in the conical-celled *nivea* flowers and 30% sucrose in the *mixta/nivea* flowers, in Eppendorf tubes held in the mouth of the flower. Landing and not drinking on the conical-celled flower or landing and drinking on the flat-celled flower were counted as correct choices. Landing and drinking on the conical-celled flower or landing and not drinking on the flat-celled flower were counted as incorrect choices (full experimental details are given in the [Supplemental Data](#)). The rationale behind this experiment was that if the bees could use tactile cues to discriminate the presence of conical cells when they landed on a flower, they would learn to leave without drinking when on a conical-celled flower but to drink when on a flat-celled flower. Under these conditions, bees readily learned to distinguish between the lines after landing. The average percentage of correct choices made during the first ten choices was $52\% \pm 5.7\%$ (data are presented as mean \pm SEM throughout) but reached $82\% \pm 4.9\%$ after twenty visits, where the curve reached an asymptote (Figure 2). Because the only difference between these flowers is the shape of their petal cells and because we have removed visual cues in the form of pigmentation, we conclude that the bees discriminate between flowers on the basis of touch.

Bees can also use this tactile cue to discriminate between biomimetic epoxy casts, which replicate with remarkable detail the differences between the conical- and flat-celled flower surfaces (Figure 1), and which have the added advantage of also lacking any biological or chemical differences that would otherwise distinguish the two surfaces. Two sets of ten individual bees were tested, again with differential conditioning. All were able to use the replicated surface structure of the epoxy flower as a cue to locate and drink from the rewarding flowers (and to avoid drinking from the adverse flowers), whether the reward was presented in conical-celled casts or flat-celled casts. Figures 3A and 3B show the total

mean learning curve for each of the sets of ten bees. When the conical-celled surface was rewarding, the average percentage of correct choices made during the first ten choices was $60\% \pm 3.3\%$ but $71\% \pm 4.1\%$ after twenty visits. The curve reached close to 100% accuracy after thirty visits. When the flat surface was rewarding, the average percentage of correct choices made during the first ten choices was $72\% \pm 4.7\%$ and reached a high level of accuracy ($89\% \pm 3.8\%$) after twenty visits. Again, the curve reached close to 100% accuracy after thirty visits (Figure 3). Because the epoxy casts differ only in their tactile properties, we conclude that bumblebees can identify and learn rewarding surfaces by touch alone.

It would therefore appear that a difference in the shape of petal epidermal cells, distinguishable only by touch, is sufficient to provide a tactile cue to bees.

Bumblebees Exhibit a Preference for Conical-Celled Epoxy Surfaces at Vertical Angles

But does the bees' ability to discriminate between the tactile cues of conical versus flat cells give us an indication of what the function of these unique petal surface structures is? Compared to visual and olfactory cues, surface structure

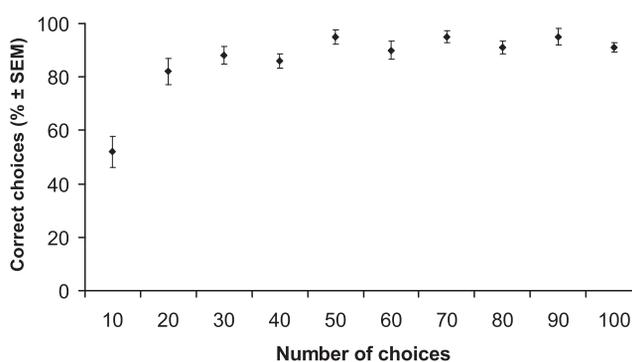


Figure 2. Learning Curve of Bees Discriminating Conical-Celled *nivea* from Flat-Celled *mixta/nivea* Flowers

Quinine solution in the *nivea* flowers, 30% sucrose in the *mixta/nivea* flowers. Landing on *nivea* and then aborting without drinking or landing on *mixta/nivea* and then drinking were considered correct choices. Number of individual bees tested (n) = 10. Error bars represent the standard error of the mean (SEM).

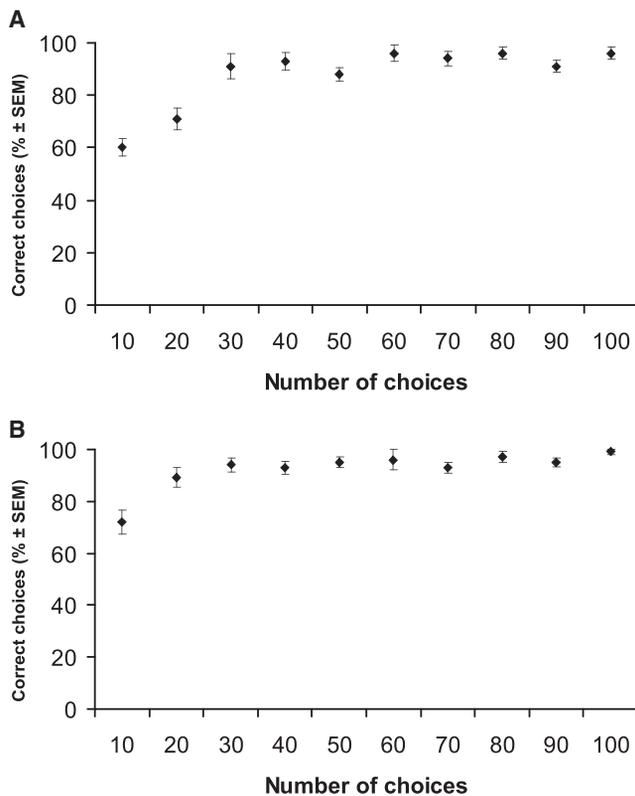


Figure 3. Learning Curves of Bees Discriminating Conical-Celled from Flat-Celled Colorless Epoxy Disks

(A) Quinine solution in the flat-celled flowers, 30% sucrose in the conical-celled flowers. Either an abort following landing on a flat-celled surface or a drink following landing on a conical-celled surface was scored as a correct choice. Number of individual bees tested (n) = 10.

(B) 30% sucrose solution in flat-celled flowers, quinine in conical-celled flowers. Either a drink following landing on a flat-celled surface or an abort following landing on a conical-celled surface was scored as a correct choice. n = 10.

Error bars represent the standard error of the mean (SEM).

would be highly inefficient as a cue to identify flowers in natural foraging—and correspondingly, conical cells would be an inefficient means for flowers to “make themselves unique.” This is because a bee can detect both visual and olfactory signals from afar, without actually alighting on the flowers, allowing the bee to veer off and search for familiar rewarding flowers after it has identified a potential target flower as unsuitable. Tactile cues, on the other hand, can only be assessed after landing and require some sampling of the surface structure before a pollinator can decide that it has landed on the “wrong” flower species. One possibility is that, in natural foraging, surface cues are not used in floral identification but instead guide the pollinator to the nectar after it has landed on the flower [3]. However, a previously unexplored hypothesis is that surface structure facilitates flower handling, by providing a better grip on otherwise slippery plant surfaces while pollinators manipulate the floral structure to extract nectar or pollen. A simple and direct method of increasing the difficulty of surface attachment is to change the angle of the surface. For this purpose, biomimetic epoxy flowers are ideal, in that large, flat artificial flowers with no alternative means of grip or attachment can be easily produced. To ensure that flower color preferences did not affect choices,

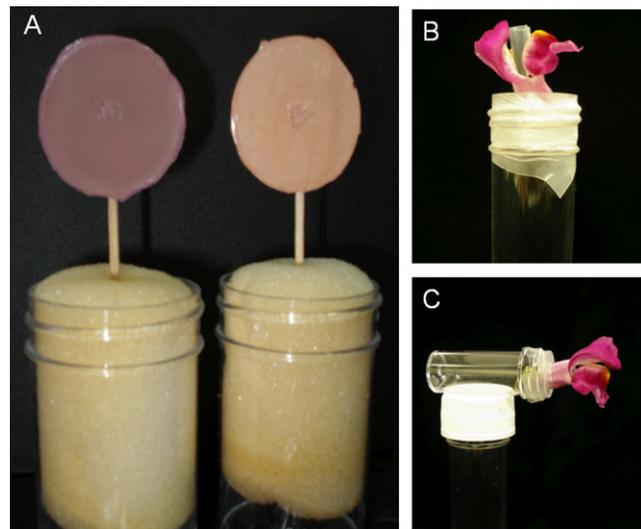


Figure 4. Experimental Positioning of Flowers and Epoxy Disks

(A) Vertical presentation of epoxy disks (in this case, purple conical-celled and pink flat-celled) to investigate innate preferences for the two surfaces. (B) Horizontal presentation of *Antirrhinum* flowers with readily accessible reward (in tube).

(C) Vertical presentation of *Antirrhinum* flowers, requiring manipulation to open the flower and access the reward at the base of the corolla.

we conducted this experiment both with conical-celled casts painted purple and flat-celled casts painted pink and with conical-celled casts painted pink and flat-celled casts painted purple (Figure 4). Rewards were provided in all casts.

When epoxy casts were presented horizontally, with the conical-celled cast purple and the flat-celled one pink, bees visited conical-celled casts $49.7\% \pm 0.93\%$ of the time. When the colors were reversed, bees visited conical-celled casts $52.3\% \pm 2.55\%$ of the time. Bees therefore showed no innate preference for either cell type if the epoxy cast was horizontal ($F_{1,36} = 1.45$, $p = 0.237$). However, once the angle of the flower increased, so did the bees’ preference for conical-celled flowers. At a vertical angle, when the conical-celled cast was purple, bees visited conical-celled casts $61.3\% \pm 1.09\%$ of the time. When the colors were reversed, bees visited conical-celled casts $62.5\% \pm 2.10\%$ of the time (Figure 5).

The effect of orientation of the flowers on bees’ preference was highly significant ($F_{1,36} = 33.71$, $p < 0.001$). Analysis of the interaction term shows that orientation of the flower does not influence color preference ($F_{1,36} = 0.03$, $p = 0.860$).

High-speed video photography of eight separate incidents of bee foraging (four on conical-celled casts and four on flat-celled casts) allowed us to capture the reason for the preference for conical cells at a steep angle. When the epoxy flower was vertical, a foraging bee had little grip and few footholds. After landing, the bee repeatedly attempted to find footholds, scrabbling particularly with the middle pair of legs. These attempts at landing on a flat-celled epoxy cast were always unsuccessful, with the feet continually slipping. However, in all recorded incidents, the bees were able to find grips on the conical-celled casts that they were not able to find on the flat-celled casts. On the conical-celled casts, all four bees were able to find sufficient grip on the “flower” that they were able to stop beating their wings and come to a “rest” position in order to feed. In all four landing attempts on flat-celled casts, the bees did not stop beating their wings and

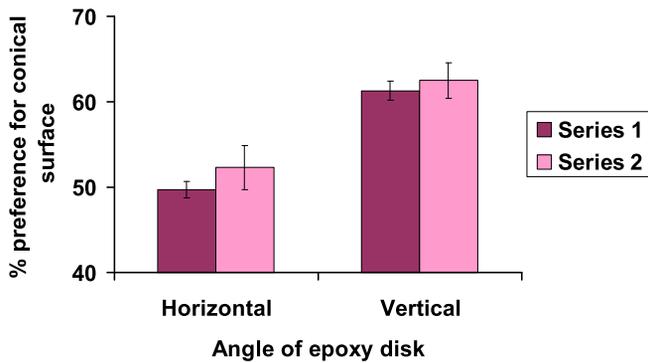


Figure 5. Preference for Conical Cells in Epoxy Disks Positioned Either Horizontal or at 90 Degrees Relative to the Horizontal

Conical flowers were colored either pink or purple and flat flowers were colored either purple or pink, to allow bees to learn to associate color with tactile effect. Two bars for each angle represent the conical = purple experiment (series 1) and conical = pink experiment (series 2), respectively. Number of individual bees tested ($n = 10$ for each color series). Error bars represent the standard error of the mean (SEM).

also continued moving their legs across the surface of the cast. In particular, the middle legs were unable to find a stable position on the flat-celled casts. Because the bees were unable to rest their wings, the energetic cost of feeding on flat-celled casts is increased relative to the cost of feeding on conical-celled casts. These videos are included as [Supplemental Data](#).

Bumblebees Exhibit a Significant Preference for Conical-Celled Flowers at Angles Difficult to Manipulate

Is this preference for conical-celled flowers when the flowers are more difficult to handle also displayed by pollinators visiting real flowers? Evidence from previous studies demonstrating that bees do show a preference for flowers with conical petal cells suggested that this could be the case. Field trials [18] showed that bees presented with the four *Antirrhinum* lines used in this study preferentially visited conical-celled *Antirrhinum* flowers. A further study with the same *Antirrhinum* lines reported that bees showed no preference for the conical-celled lines if they were unable to touch the flowers [22]. This therefore suggests that the visual signal of the color difference between the pigmented wild-type and *mixta* mutant lines does not cause the avoidance of the flat-celled mutant lines demonstrated previously [4, 18, 24], and we have eliminated the possibility of an olfactory preference in this study. In another previous study, it was also shown that although bees had no apparent preference for either of the colors shown by the two lines, they could discriminate between them [22]. Bees therefore appear to be able to use the difference in color as a cue to distinguish between the two lines when it is advantageous for them to be able to do so. However, the nature of that advantage was unknown before the present study. To establish whether this advantage involves the increased handling ability identified via epoxy replicas, pigmented *Antirrhinum* flowers (conical-celled wild-type and flat-celled *mixta* mutant) were used to allow bees to learn the color difference as a visual cue. Equal rewards were presented in all flowers. When the flowers were horizontal and required little or no handling (Figure 4B), the bees visited (landed on) wild-type flowers $51.3\% \pm 2.31\%$ of the time. However, when the flowers were vertical and required

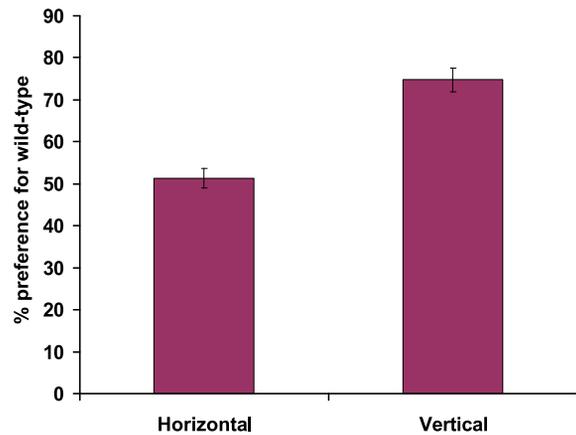


Figure 6. Preference for Landing on Wild-Type Conical-Celled Flowers over *mixta* Flat-Celled Flowers at Two Angles, with Both Flower Types Equally Rewarded

Number of individual bees tested ($n = 10$; 100 choices per bee). Error bars represent the standard error of the mean (SEM).

complex manipulation to open (Figure 4C), bees landed on the wild-type flowers $74.8\% \pm 2.79\%$ of the time (Figure 6). Individual bees showed a significant increase in preference for wild-type flowers when the flowers were presented vertically ($t_{18} = 6.931$, $p < 0.001$, using arcsine-transformed proportions of an individual's total visits made to the wild-type flower). This marked change in preference for conical-celled flowers when the angle of the flower is the only variable strongly points to a lack of grip as explaining the preference of bumblebees for conical-celled flowers, an effect which is likely to be particularly strong in flowers requiring any degree of manipulation to open, such as *Antirrhinum* or *Aconitum* [25, 26].

This grip advantage is unlikely to be the only function of conical cells, which are also present on flowers pollinated by hovering pollinators such as moths. However, there is evidence that these cells also play important roles in floral color, shape, and temperature, which may be variably significant in different ecological situations [1, 4, 16, 18].

Bumblebees Take Longer to Decide to Abort from Flat-Celled Flowers but Abort from Them More Frequently

Our study also suggests that as well as discriminating before landing using the visual color cue, bees also discriminate against flat-celled flowers after landing, possibly then using the tactile properties of the flower as an additional cue. Bee behavior on the *mixta* mutant and wild-type flowers was observed and timed, because flower preferences have previously been linked to handling difficulty and longer handling times [15, 27]. For a bee to land and successfully enter the flower and drink took an average of 19.5 ± 2.68 s on a wild-type flower and 19.8 ± 3.03 s on a *mixta* flower. Bees that did not successfully enter the flower but instead aborted without drinking took on average 2.4 ± 0.50 s before aborting a wild-type flower and 3.2 ± 0.38 s before aborting a visit to a flat-celled *mixta* flower.

This analysis determined that the only factor that had a significant influence on time spent on the flower was whether the bee drank or decided to abort ($F_{1,57} = 90.89$, $p < 0.001$), but neither flower type ($F_{1,57} = 0.22$, $p = 0.640$) nor the interaction between decision and type ($F_{1,57} = 0.19$, $p = 0.668$) had any effect. These data are supported by previous field trials showing that bees are more likely to abort flat-celled *mixta*

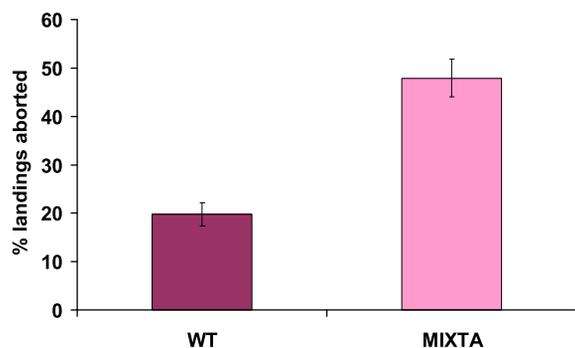


Figure 7. Postlanding Abortion of Visits to Wild-Type Conical-Celled Flowers and *mixta* Flat-Celled Flowers Held Vertical, with Both Flower Types Equally Rewarded

Number of individual bees tested (n) = 10 bees; 100 choices each. Error bars represent the standard error of the mean (SEM).

flowers both before (perhaps using the learned color cue) and after (perhaps using the tactile cue) landing [4].

We also analyzed what proportion of bee visits to either flower type resulted in a successful forage (i.e., the collection of sucrose solution) versus what proportion of visits were aborted. On the wild-type flowers, bees aborted without drinking after landing on a flower 19.8% (SEM = 2.38%) of the time. On the *mixta* flowers, bees aborted after landing 47.9% (SEM = 3.88%) of the time. Therefore, bees abort without drinking significantly more frequently from the flat-celled *mixta* mutant than from the conical-celled wild-type flowers (Figure 7).

Although we found that there is no difference in handling times when flowers are successfully manipulated, the ability of a bee to find a foothold and relax its beating wings would mean that the pollinator could expend less energy foraging on conical-celled flowers and so would have a higher net rate of energy intake on conical-celled flowers than on flat-celled flowers. The lack of difference in handling times for pollinators on conical- versus flat-celled flowers also suggests that the motor skills that must be learned in order to open the flower are the same irrespective of cell shape, again suggesting that the lack of grip on flat-celled flowers is the reason for pollinator discrimination against flat-celled flowers.

Conclusions

The hypothesis that the development of specific specialized structures on the petal epidermis is adaptively significant is confirmed in this example of conical cells. The restriction of conical cells to the petal led to the suggestion that they are involved in pollinator attraction, because that is the primary function of petals. We have shown that this hypothesis is correct. The tactile properties of conical cells can act both as a cue and as a handling advantage to pollinators, aiding efficient foraging and therefore the transfer of pollen. It will be informative to relate the presence of conical petal cells to the angle of floral presentation and method of pollinator manipulation in a range of angiosperm species.

Experimental Procedures

Plant Material

Isolation of the isogenic wild-type (Mx^+/Nv^+), *mixta* (mx^-/Nv^+), *nivea* (Mx^+/nv^-), and *mixta/nivea* (mx^-/nv^-) lines was as described in [18]. In Antirrhinum, the *nivea* mutation results in white flowers (Figure 1) because of lack of chalcone synthase, the enzyme required for the first step in flavonoid

biosynthesis [28]. The *nivea* mutant therefore lacks not only magenta anthocyanins but also ultraviolet-absorbing pigments. The flat-celled *mixta/nivea* double mutant is indistinguishable from the conical-celled *nivea* mutant to the human eye [18].

Biomimetic Replication of Petal Surface Textures

The replication of floral surfaces was achieved via a modified version of the methods detailed in [29] (see Supplemental Experimental Procedures).

Bumblebee Experiments

Bumblebee experimental conditions are detailed in the Supplemental Experimental Procedures. Naive *Bombus terrestris* colonies were supplied by Syngenta Bioline (UK).

Bumblebee Discrimination between Conical- and Flat-Celled Surfaces

To determine whether bees could distinguish between conical- and flat-celled surfaces of both artificial epoxy flowers and *nivea* (white) Antirrhinum flowers, differential conditioning was used [23] (see Supplemental Experimental Procedures). In both cases, a single trial consisted of releasing a marked bee from the colony and allowing it to forage until satiated. Ten bees were tested, each to 100 choices. A choice was counted as when the bee landed on a flower and either drank or left without trying to drink (aborted). Either 30% sucrose (rewarding flower) or a 0.12% solution of quinine hemisulfate salt in water (unrewarding flower) was present in alternate flower types. Landing and drinking on the rewarding flower or landing and not drinking on the unrewarding flower were counted as correct choices. Landing and not drinking on the rewarding flower or landing and drinking on the unrewarding flower were counted as incorrect choices. During a trial, flowers containing sucrose were refilled once the forager had left the flower and landed on an alternative flower. Between trials, flowers were cleaned with 30% ethanol to remove scent marks and moved in a pseudorandom pattern to prevent bees from associating reward with a specific location.

Bumblebee Preference for Conical-Celled Surfaces at Different Angles

Fully pigmented *mixta* and wild-type Antirrhinum flowers were used so that the color difference could act as a visual cue. Epoxy disks were painted on the back with two colors (pink and purple) that bees show no strong preference between but can discriminate [22]. To investigate preferences, flowers were presented with equal sucrose reward in both flower types held either horizontally or at a 90° angle. At both angles, ten bees were tested individually to 100 choices. A landing on a flower was recorded as a choice, and in the case of landings on the Antirrhinum lines, any subsequent bee behavior was also recorded. Images of bee foraging behavior on the epoxy flowers were recorded with a Fastec TroubleShooter TS1000MS monochrome high-speed video camera.

Supplemental Data

The Supplemental Data include Supplemental Results, Supplemental Experimental Procedures, one figure, and seven movies and can be found with this article online at [http://www.cell.com/current-biology/supplemental/S0960-9822\(09\)01050-1](http://www.cell.com/current-biology/supplemental/S0960-9822(09)01050-1).

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