



Honey bees switch mechanisms to drink deep nectar efficiently

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The feeding mechanisms of animals constrain the spectrum of resources that they can exploit profitably. For floral nectar eaters, both corolla depth and nectar properties have marked influence on foraging choices. We report the multiple strategies used by honey bees to efficiently extract nectar at the range of sugar concentrations and corolla depths they face in nature. Honey bees can collect nectar by dipping their hairy tongues or capillary loading when lapping it, or they can attach the tongue to the wall of long corollas and directly suck the nectar along the tongue sides. The honey bee feeding apparatus is unveiled as a multifunctional tool that can switch between lapping and sucking nectar according to the instantaneous ingesting efficiency, which is determined by the interplay of nectar–mouth distance and sugar concentration. These versatile feeding mechanisms allow honey bees to extract nectar efficiently from a wider range of floral resources than previously appreciated and endow them with remarkable adaptability to diverse foraging environments.

honey bee | insect mouthparts | feeding strategies | plant–pollinator interactions | fluid mechanics

Over evolutionary time, fluid-feeding insects on our planet have achieved unprecedented success. More than half of all known insects on Earth—over 500,000 species—are fluid feeders (1). Among them, nectar feeders have attracted the attention of scientists since Darwin predicted, well before its discovery, the existence of a specific orchid corresponding to the extraordinarily long proboscis of sphinx moth (2, 3). How nectar-feeding insects use their elaborate mouthparts to interact with the great variety of flower structures remains an important question in evolutionary biology, ecology, and biomechanics (4–7). One crucial aspect of plant–pollinator interactions is the size and shape matching between the floral corolla/nectar chamber and the mouthparts of the pollinator (8). From the nectarivore’s perspective, foraging efficiency, the main driver for such matching, is constrained by the accessibility and amount of floral reward (9). For instance, handling time increases when the nectar is located deep inside the corolla, while more easily accessible shallower flowers usually have smaller rewards (10, 11). Thus, assessments of the importance of feeding mechanisms should consider both ingestion efficiency and reward accessibility, especially in the context of explicit fluid–mouthparts interactions within the nectar reservoir (11–16). These interactions are crucial for our understanding of the links between physical principles and the adaptations of both plants and pollinators that shape ecological communities.

Honey bees (*Apis mellifera*) are among the most important pollinators in the world, and they are excelled in foraging a very wide spectrum of floral nectars, including highly concentrated ones (17). They have elongated proboscides which are made of a pair of galea and labial palpi that form a feeding tube surrounding a hairy glossa or tongue (18, 19) (Fig. 1 *A* and *B*). The honey bee’s tongue, decorated by transverse rings of cuticle each bearing thin hairs, is the main feeding structure for extracting the nectar in the floral tube (20). Lapping, i.e., the feeding mechanism that has been extensively studied for honey bees (21–23), involves back-and-forth motion of the tongue to collect nectar. We have recently shown, however, that honey bees exhibit an alternative feeding strategy involving direct suction through their proboscides (24). They are able to employ suction, by immersing the “proboscis tube” formed by the proximal mouthparts (Fig. 1 *B*), when ingesting low-viscosity nectar (<30% w/w), and switch to lapping for higher concentrations (24). The volitional switching of feeding patterns according to the liquid properties allows them to efficiently exploit various floral nectars and enhances their adaptability to a wide range of energy sources.

All previous studies on honey bee feeding mechanisms have been conducted *in vivo* but under the unnatural condition of virtually unlimited supplies of nectar (5, 24–26). Such large nectar pools are rare in the flowers they visit in the wild. For example, in the bee-pollinated flora of Mediterranean shrublands, plants produce less than 0.5 μL of nectar

Significance

The match between flower and nectar-eaters’ mouthparts is assumed as a main factor affecting the interactions between plants and their pollinators. However, the efficiency at which nectar can be depleted at different depths inside a floral tube determines resource access and profitability. Honey bees’ feeding mechanism has long been studied but under the unnatural condition of virtually unlimited nectar supplies. Here, we show that honey bees are able to switch between lapping and sucking according to the amount of nectar acquired, which is determined by the interplay of nectar–mouth distance and sugar concentration. This expands the expected spectrum of floral lengths at which honey bees can forage profitably, demonstrating the importance of functional rather than shape-only matching in plant–pollinator interactions.

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(27), and in many flowers, these rewards are found deep inside floral tubes (e.g., Fig. 1A). Higher volumes may be available in less arid regions, but evaporation and frequent visits by nectarivores lead to large diurnal variation in reward volumes and concentrations (17, 28). How far a nectar eater can reach within a flower influences the net gain of a given visit, consequently shaping resource exploitation by competing nectarivores and plant–pollinator interactions (9). If honey bees were only able to suck nectar when the proboscis tube tip is immersed in the nectar, this would greatly limit their nectar extraction abilities in low-viscosity rewards (24), especially when competing with other insects with longer mouthparts. The honey bee tongue can protract beyond the proboscis tube to access deeper nectar, but anatomical descriptions of the mouthparts concluded that the tongue does not serve for direct intake of liquids by suction (18), and there is no evidence of nectar transport through the glossal lumen (29). Alternatively, the nectar could be reached with the extendable tongue for lapping, but this would mean longer handling times and more energy invested due to the back-and-forth motion, reducing the net gain. In distant nectar pools, lapping efficiency would be also diminished because the immersed portion of the tongue is reduced as the nectar meniscus recedes upon pool depletion. Here, we study the feeding behaviors of honey bees ingesting nectar inside a corolla-like feeding tube, with a receding meniscus [as opposed to maintaining the meniscus in contact with the proboscis tube (26, 30)], thus imposing similar biophysical constraints to the ones honey bees face in nature. We uncover the multiple methods used by honey bees to feed on distant nectar and elucidate the mechanism switches that shape their feeding strategy preferences. The accessibility of the caloric reward influences the effectiveness of the extraction mechanism and ultimately the foraging efficiency that shapes large-scale ecological interactions (e.g., pollination networks).

Results

Drinking Strategy Alternation along Corolla Depth. To visualize the mouthpart movements of honey bees feeding on nectar in an artificial corolla, we fed prestarved bees with blue-dyed sucrose solutions of three concentrations ($c_s = 10\%$, 30% , and 50% w/w) contained in a capillary tube (inner diameter: 1.4 mm) (Fig. 1C and Movie S1). The position of the tongue tip, the galea tip, and the meniscus at the liquid–air interface were measured as a function of time. When the bee was offered low sucrose concentration (10% w/w) nectar, it plunged the proboscis into the nectar and kept the tongue protracted sucking the liquid until the meniscus was inaccessible to the very tip of the tongue (Fig. 1D). When bees fed on 30% w/w sucrose solution, they first lapped the liquid at a frequency of $f = 3.1 \pm 0.8 \text{ s}^{-1}$. However, as the liquid was depleted in the capillary, the bees significantly slowed down the tongue movements until a gradual transition to suction is observed (when the meniscus depth increased to ~ 5 mm, tongue frequency $f < 1 \text{ s}^{-1}$, Fig. 1E and G). The tongue reciprocation frequency further reduced to 0.2 s^{-1} at a meniscus depth of 7 mm (Fig. 1G), indicating only occasional retractions of the tongue. The shift in mechanism occurs gradually by making longer and longer pauses at the end of each cycle when the tongue is at maximum protrusion, starting around 4 to 5 mm of meniscus depth (e.g., Fig. 1E). When feeding on 30% concentration, 82% of the tested bees employed lapping when the liquid was close to the proboscis base (meniscus depth < 5 mm), and 95% of the tested bees transferred to sucking when the liquid was far from the mouth base (meniscus depth > 5 mm) (Fig. 1H). Some bees would retract the tongue at random liquid positions when sucking; hence, the measured tongue frequency can still be

>0 for 10% and 30% feeding trials (Fig. 1G). When exposed to higher concentrations (50% w/w, 0.012 Pa s), the bees exhibited faster initial tongue reciprocation (Fig. 1G) and kept lapping until the tongue could not reach the liquid (Fig. 1F). These results indicate that bees are able to make full use of the mouthpart lengths (including tongue extension) during both lapping and suction. In the experiments with 50% concentration solutions, the tongue frequency showed a clear decrease when the meniscus recedes deeper inside the corolla but still maintained a lapping pattern (Fig. 1F and G). This small decrease of frequency is likely related to the increase in tongue extension, but it is much smaller than the frequency reduction in 30% solutions related to the occurrence of “pauses for suction” when the tongue is fully extended (Fig. 1G).

We highlight that nectar concentrations around 30% w/w are very common in the flowers that honey bees feed from [the observed average nectar concentration for bee-pollinated plants is 35% w/w (31)]. Given that for bumble bees (*Bombus terrestris*), we did not find the ability of switching feeding mechanisms according to the nectar viscosity (30), we decided to test whether they were capable of modulating their mechanics according to liquid distance, using the nectar concentration (10% w/w) where honey bees almost exclusively used suction (Fig. 1D, G, and H). For bumble bees, only lapping was observed ($n = 10$, Movie S2), underscoring the special feeding capabilities of honey bees. To uncover the underlying factors that drive these mechoethological adjustments in honey bees (32), we examined in detail the feeding biomechanics and hydrodynamics for lapping and suction modes. We focus on how bees can access and extract liquid when only the tongue tip is in contact with the fluid (puzzling given the apparent lack of ability to move fluid within the tongue), which has never been described before.

Sucking Nectar in Deep Corolla Tubes. Suction in honey bees has been assumed to be actuated through expansion of the cibarial pump in the head, but this has never been corroborated. Using Synchrotron X-ray microscopic imaging, we found that as the airtight pump in the head expanded through contraction of the pump dilator muscles, nectar was forced through the feeding channel to fill the expanding pump chamber (Fig. 2A and Movie S3). The fluid is set in motion thanks to the pressure difference between the atmosphere and the internal pump cavity (33). Then, a valve at the hypopharynx closes, and the pump contracts to transport the liquid food into the esophagus (Fig. 2B). The typical time variation in pump diameter (Fig. 2C), measured at the center of the pump, reveals a regular motion of the cibarial pump and explains the staircase pattern of the liquid meniscus movement during honey bee sucking nectar in the feeding tube (Fig. 1D).

We found that honey bees can suck nectar deep inside corollas even when the proboscis tube tip is not in contact with the fluid (Fig. 1 and Movie S1). Therefore, it remains unknown how they can transfer the pressure difference generated in the cibarial pump all the way to the tongue tip deep inside the corolla. Coupling a high-speed camera to a microscope, we found that once the meniscus receded past the apical end of the proboscis tube (galea tip), all tested honey bees make a close contact of their tongue with the corolla wall and extend their tongues further, exhibiting a distinct elongation in relation to the galea tip ($n = 15$) (Fig. 2D and Movie S4). The tongue–wall structure forms a kind of capillary bridge—as an open liquid channel (34)—allowing the transport of nectar along its sides (Fig. 2D). We performed particle image velocimetry (PIV) analysis by adding particles to the nectar, which shows that a rivulet runs from the liquid source to the proboscis, with the flowing direction being parallel to the tongue (Fig. 2E). The velocity of the particles was symmetrically

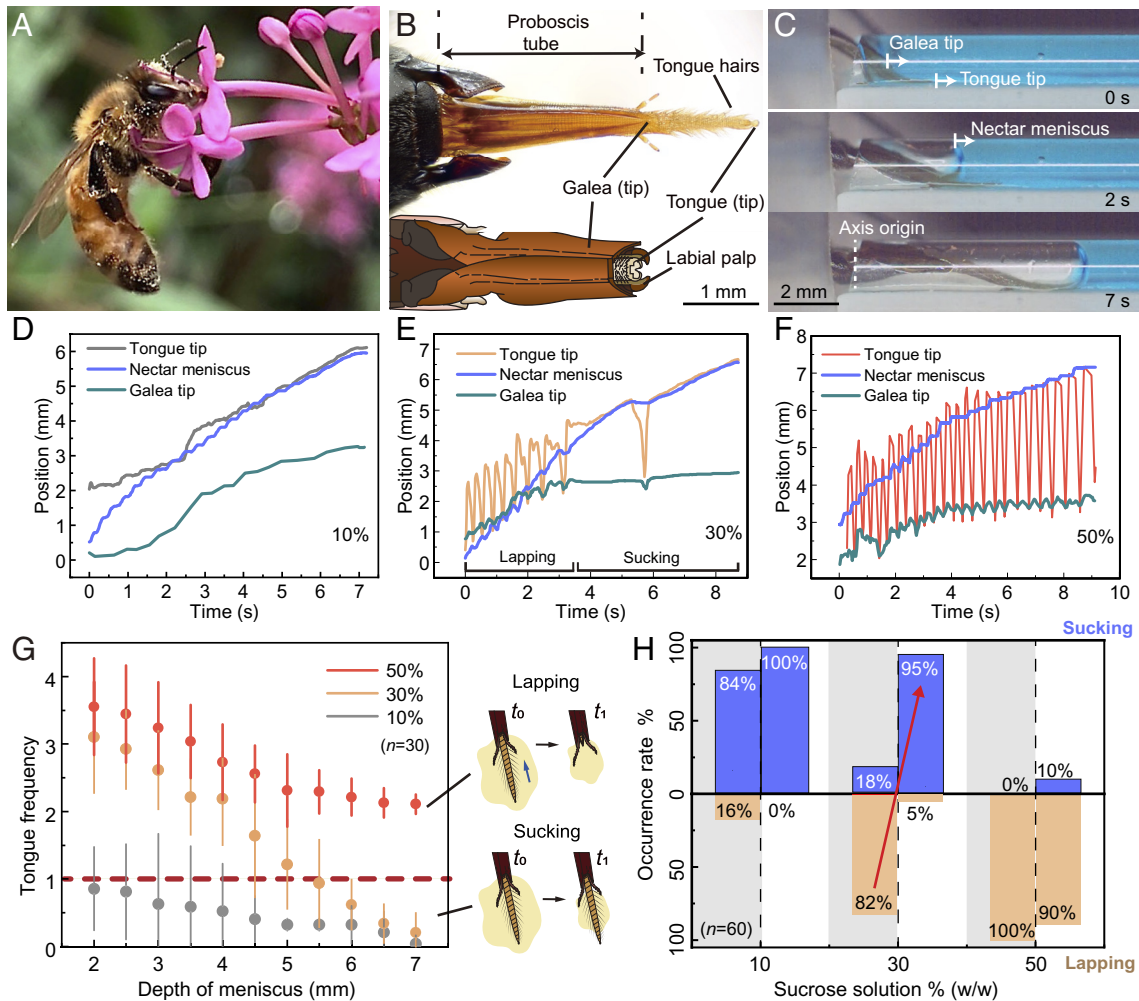


Fig. 1. Honey bees feeding in a corolla tube with depleting meniscus at different concentrations. (A) Honey bee foraging for nectar inside a long corolla of *Centranthus ruber*. (B) Image and schematic of bee mouthparts. A pair of galea and labial palpi together form the proboscis tube. The bee's tongue (glossa) can protract beyond the apical end of the tube. (C) Snapshots of a honey bee feeding on 30% w/w blue-dyed sucrose solution in an artificial corolla tube. (D–F) Typical movement patterns of the tongue tip, galea tip, and nectar meniscus in the tube, when honey bees fed on 10%, 30%, and 50% w/w sucrose solutions, respectively. (G) Tongue frequency in relation to the depth of meniscus. The red dashed line denotes the critical tongue frequency used to classify sucking (tongue frequency $f < 1 \text{ s}^{-1}$) or lapping ($f > 1 \text{ s}^{-1}$). Schematics depict sucking and lapping patterns of the honey bee ingesting nectar. Sample size $n = 30$ individuals, error bars are SD around averages. (H) Occurrence of sucking and lapping feeding modes in honey bees, when feeding on sucrose solutions with the meniscus depth close to the proboscis tube base (meniscus depth $< 5 \text{ mm}$, gray shade) or far from the proboscis base (meniscus depth $> 5 \text{ mm}$, white background). Sample size $n = 60$ individuals.

distributed on the two sides of the tongue and the u component of velocity in the transverse section (green dashed line in Fig. 2E) reached a peak around 0.01 m/s ($n = 10$), and the average velocity u of the fluid is close to 0.001 m/s ($n = 10$) (Fig. 2F). Considering the very low Bond numbers for this system $Bo = \rho_l g R_c^2 / \gamma \ll 1$ [where ρ_l is the density of the fluid, g the gravitational acceleration, R_c the proboscis radius, and γ the liquid surface tension (SI Appendix)], the gravitational effect is negligible and nectar can flow on the upper corolla wall (5, 35).

Besides the stability of the deep nectar sucking, the feeding rate (energy gain per unit time) is another factor that could affect the foraging behavior of bees (24, 36). We examined the feeding behavior of honey bees by investigating the change in volumetric intake rate Q ($\mu\text{L/s}$), which is proportional to the net energy gain per unit time $Q = E / \rho_l c_s c_l$ with the concentration [the energy spent is too small to be considered (36)], where $c_l = 1.54 \times 10^7 \text{ J/kg}$ is the energy content per unit mass of sugar (37). When sucking, the maximum velocity of the meniscus decreases as the depth of the liquid increases, indicating that the distance to the liquid

source has a significant influence on the feeding rate (Fig. 2G). We have previously examined the sucking mechanism for honey bees using their proboscis tube only (30). The sucking flow rate can be expressed by

$$Q_1 = \frac{\pi}{24} \frac{\Delta P (R_c^4 - R^4)}{\mu L} \frac{h^2}{R^2}, \quad [1]$$

where ΔP is the pressure difference between the pump and the liquid source, μ the liquid viscosity, L the characteristic length of the flow distance in the proboscis tube, R the inner radius of the tongue, and h the average spacing between two hairs of the tongue. As the sucrose concentration c_s of nectar increases linearly, its viscosity μ grows exponentially (SI Appendix). Eq. 1 is a Poiseuille-like expression where the geometric factor $h/R \ll 1$ takes into account the presence of hairs which impacts the flow rate. It describes the nectar sucking with the proboscis tube; however, liquid can also flow through the tongue at a free surface when sucking liquid deep in the capillary tube (Movies S4 and S5).

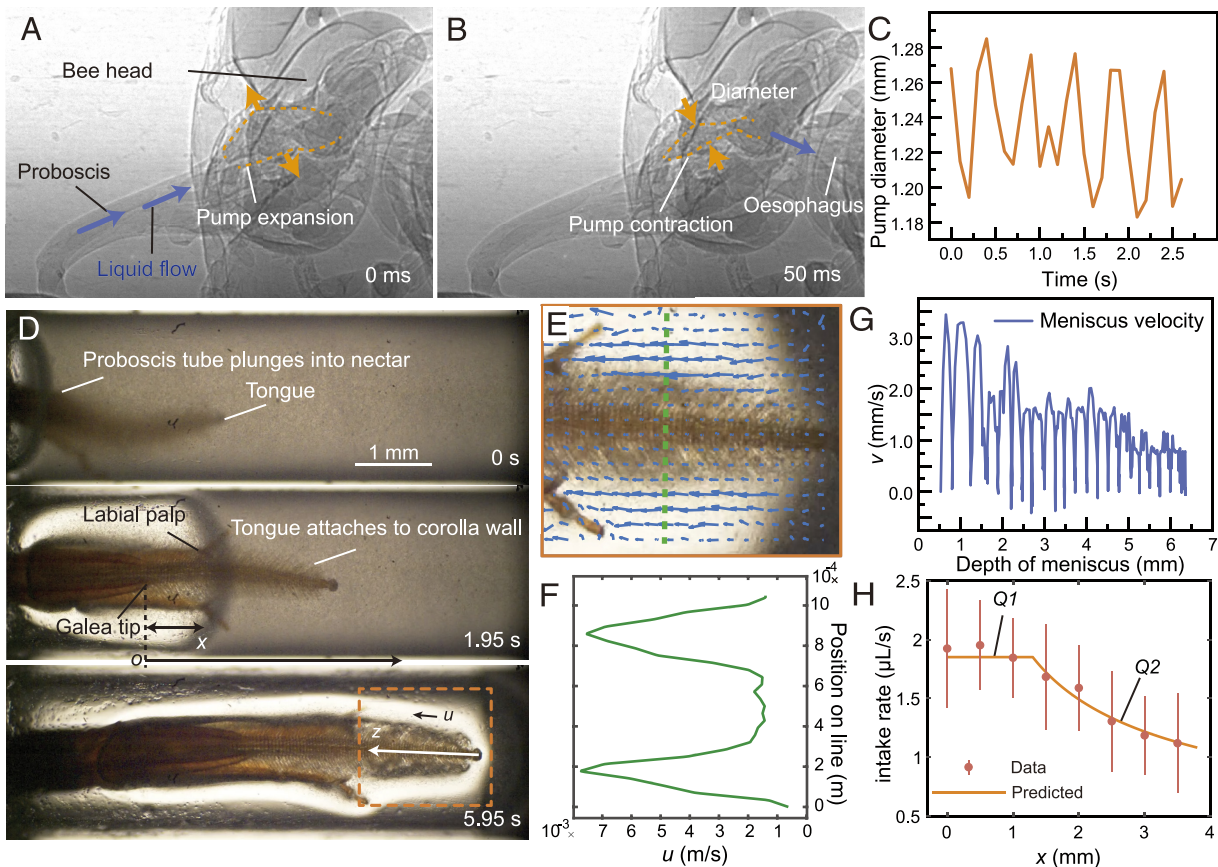


Fig. 2. Suction mechanism of honey bees to extract nectar deeper in the corolla. (A) Frames from a synchrotron X-ray video of a honey bee sucking 30% nectar through the expansion of the head pump. Dotted orange lines indicate the boundaries of the cibarial pump cavity, and blue arrows indicate the direction of the nectar flow. (B) Contraction of the head pump as the liquid is swallowed. The orange arrows point at the measured pumped diameter. (C) Variation of the diameter of the head pump at its center as a function of time during the feeding process. (D) Microscopic view of a honey bee sucking sucrose solution ($c_s = 20\%$ w/w), from the proboscis totally plunged at 0 s to the maximum accessible distance at 5.95 s. The o axis originates from the galea tip, and x denotes the liquid distance with respect to o . The z axis is set along the tongue, and u denotes the liquid velocity parallel to z . (E) PIV results for the rectangle area in panel D, with arrows indicating the velocity direction and magnitude. (F) The distribution of velocity u at the green dashed line in panel E. (G) Typical liquid meniscus velocity as a function of meniscus level during honey bee sucking. The meniscus velocity was derived from the time-position data in Fig. 1D. (H) Data and theoretical prediction of the intake rate (measured in $\mu\text{L/s}$) in each pumping event as a function of liquid distance x ($c_s = 10\%$ w/w, $\mu = 0.0012$ Pa s) ($n = 10$); error bars are SD around averages.

When the liquid distance x (Fig. 2D) increases beyond a critical value $x^* = L$, the flow rate in the free surface region becomes smaller than Q_1 and thus will thus determine the global flow rate (SI Appendix, Fig. S1), which writes

$$Q_2 = \frac{\pi}{24} \frac{\Delta P (R_c^4 - R^4)}{\mu x} \frac{b^2}{R^2}. \quad [2]$$

Hence, the effective sucking flow rate of the whole process can be expressed as $Q_{\text{suck}} = \min(Q_1, Q_2(x))$. In order to apply Eqs. 1 and 2 to describe suction by honey bees, we need to know the pressure difference, ΔP , generated by the head pump. Since there are no relevant reports for honey bees, we use data obtained for butterflies to estimate this pressure difference. By measuring the dependence of flow rate on sugar concentration, Pivnick and McNeil inferred that butterflies apply an essentially constant suction power \dot{W} while drinking, regardless of the nectar concentration (38) with values given by $2.2 \times 10^{-7} \text{ J} \cdot \text{s}^{-1} \leq \dot{W} \leq 4.6 \times 10^{-7} \text{ J} \cdot \text{s}^{-1}$ at $T = 25^\circ \text{C}$ when the concentration varies from 10 to 65%, i.e., when viscosity varies by two orders of magnitude, $10^{-3} \text{ Pa} \cdot \text{s} \leq \mu \leq 10^{-1} \text{ Pa} \cdot \text{s}$. If we assume that \dot{W} is also essentially constant for bees, i.e., $\dot{W} = Q_{\text{suck}} \Delta P = \text{const.}$, we obtain the expression of

ΔP in terms of \dot{W} . Substituting this last relation into Eqs. 1 and 2, we obtain

$$\begin{cases} Q_1 = \left[\frac{\pi}{24} \frac{\dot{W} (R_c^4 - R^4)}{\mu L} \right]^{\frac{1}{2}} \frac{b}{R}, \\ Q_2 = \left[\frac{\pi}{24} \frac{\dot{W} (R_c^4 - R^4)}{\mu x} \right]^{\frac{1}{2}} \frac{b}{R} \end{cases}. \quad [3]$$

Therefore, the liquid intake rate decreased when the liquid meniscus level x is larger than: $Q_{\text{suck}} = Q_2 \sim x^{-1/2}$. Eq. 3 contains no fitting parameters once the physiological parameters are fixed by experimental measurements. We used the following physiological values: $R = 70 \mu\text{m}$, $b = 20 \mu\text{m}$, and $R_c = R + L_b \sin(\theta) = 217 \mu\text{m}$, where $L_b = 180 \mu\text{m}$ and $\theta = 55^\circ$ are the length and the maximum erection angle of the tongue hairs, respectively (30). The characteristic length of the flow distance in the proboscis tube L is 1.3 mm, at which distance, the flow rate began to decrease (Fig. 2H). For the suction power \dot{W} in Eq. 3, we simply use the lower boundary value reported for butterflies, since the honey bees

are smaller (38). Therefore, we get $Q_2 = 2.11 x^{-1/2}$ for honey bee feeding 10% nectar ($\mu = 0.0012 \text{ Pa s}$), where x is measured in mm and Q_2 in $\mu\text{L/s}$. As shown in Fig. 2H, Eq. 3 quantitatively agrees with the data, supporting the proposed model for suction (Fig. 2H).

Lapping Nectar in Deep Corolla Tubes. Previous studies have examined honey bee lapping when their tongues have been fully immersed in the nectar. Here, we investigated lapping on a receding meniscus (as it would occur in natural flowers) focusing on the capture of deep nectar at a 50% w/w concentration, i.e., without the use of suction (Fig. 1 F–H). The microscopic high-speed videos unravel four stages for the lapping process: 1) tongue protrusion, 2) hairs unfolding to load nectar, 3) tongue retraction into the proboscis tube, and 4) offloading the nectar and swallowing. We define $T_i (i = 1-4)$ as the time elapsed in each phase (Fig. 3 A and B and Movie S6). Notably, during the loading process, the hairs unfolded asynchronously along the tongue. As soon as the distal tongue hairs touch the nectar, they unfolded first, and then, the rest of the hairs along the tongue unfolded sequentially toward the proximal end (Movie S6). This asynchronous erection pattern contrasts with the situation when the tongue is fully plunged into a nectar pool; in the latter, the hairs on the proximal segment erect earlier than those on the distal end of the tongue (22). The PIV analysis shows that the fluid rose through the open channels formed between the tongue and the tube wall, which suggests that the flow is driven by capillary forces (Fig. 3 A and D). Previous research had found a precursor liquid film (potentially saliva) on the tongue surface, which should be able to render the tongue perfectly wettable when getting into contact with the liquid food, facilitating this capillary loading process (39).

Honey bees did not protract their tongues to the furthest extendable position when the liquid level was close to the mouth, but instead, they gradually reached deeper positions as the liquid food was depleted in the tube (Fig. 1). We found that the maximum tongue tip position $x_m = \text{Max}(x_{\text{tip}})$ at each lapping event exhibited a linear increase with an increased in the distance of the liquid ($n = 10$), which can be described by $x_m = a_t x + b_t$, where x is the liquid distance from the galea tip (a fixed point on the mouth), $a_t = 0.51$, and $b_t = 1.43 (R^2 = 0.97)$, x_m , and x are measured in mm, Fig. 3E). The position of the base of the tongue when fully extended, i.e., when its tip is at a position x_m , is given by $x_{\text{base}} = x_m - L_{\text{tongue}}$, where $L_{\text{tongue}} \cong 3.5 \text{ mm}$ is the length of the tongue. Note that because the position of the base of the tongue is always located behind the galea position, we have $x_{\text{base}} < 0$, see Fig. 3C.

The ingestion rate of lapping can be calculated as $Q_{\text{lap}} = V_{\text{lap}} / T_{\text{lap}}$, where V_{lap} is the captured liquid volume per lap, and the $T_{\text{lap}} = \sum_{i=1}^{i=4} T_i$ is the consumed time per lap. The protraction of the tongue relies on the internal elastic tongue rod (40), and we found that the protraction time T_1 increased very slightly as the liquid level dropped (Fig. 3G). The retraction of the tongue depends on the contraction of the retraction muscle, and the retraction time T_3 does not change significantly either (Fig. 3G), which confirms that bees are able to adjust their tongue retraction force (26). Similarly, the interval time T_4 for swallowing decreased only slightly with x , which could result from the decrease in load volume (Fig. 3I).

In contrast, the time spent in the loading phase increased significantly as the liquid went deeper (Fig. 3F). The loading time should be dominated by two main aspects: the time required to

ensure the hair relaxation in the liquid T_{rel} and the time for the nectar to flow from the pool to the tongue base driven by capillary force T_{cap} . It has been previously shown that the tongue hairs relaxation dynamics in a viscous liquid can be expressed as $t = \left[1 - \left(1 - d(t)/d_m \right)^{1/11} \right] T$, where $T = 4.35 \left[\frac{\mu^{10} d_m}{(E_b R_b^4 / L_b^4) v_c} \right]^{1/11}$

is the total relaxation time when hairs reach their maximal extension, $v_c = \frac{4\mu}{\rho_l R_b}$, $d(t)$ is the distance between the tip of the hair and the tongue, $d_m = L_b \sin(55^\circ)$ is the maximum lateral extension of the tip of the tongue hairs, and $E_b = 1.1 \text{ MPa}$ and $R_b = 2.7 \mu\text{m}$ are the Young modulus and radius of the tongue hairs (26). Here, we estimated the hairs relaxation time when hairs reached $f_r = 95\%$ of its maximum position d_m , namely $T_{\text{rel}} = t_{95} \cong 0.24 T$ when $d(t_{95}) = 0.95 d_m$ (SI Appendix, Fig. S2). As the liquid distance increased, less of the tongue was immersed, and a larger portion should be filled by capillarity. We proposed to estimate the time of the capillary-dominant loading process through the Lucas–Washburn law, which yields $T_{\text{cap}} = \frac{2\mu}{\gamma b} x^2 + t_c$, where x denotes the distance from the liquid meniscus to the tongue base, b is the hair spacing as the characteristic width of the liquid channel, $\gamma = 0.05 \text{ N/m}$ is the liquid surface tension, and $t_c \cong 55 \text{ ms}$ is a short pause after hairs full extension (Fig. 3B). The time required to fill the tongue with the liquid should be dominated by the process that takes the most time, i.e., $T_2 = \max(T_{\text{rel}}, T_{\text{cap}})$. The observed evolution of T_2 agrees with these relations (Fig. 3F). Since the time spent in other phases only changed very slightly with the liquid level (Fig. 3H), we can estimate the time of each lapping motion as $T_{\text{lap}} = \max(T_{\text{rel}}, T_{\text{cap}}) + c$, where $c = T_1 + T_3 + T_4 \cong 210 \text{ ms}$. We expect this value to be constant across concentrations since viscous drag may have insignificant effects in these three phases. The predicted result T_{lap} fits well the experimental data (Fig. 3H).

The volume per lap is another important parameter that can be expressed by $V_{\text{load}} = V_{\text{dip}} + V_{\text{cap}}$, where $V_{\text{dip}}(x) = \pi \left((R + f_r d_m)^2 - R^2 (x_m - x) \right)$ denotes the liquid volume collected by the immersed portion of the tongue, and V_{cap} is the liquid volume loaded through capillary flow. We note that not all the periphery of the tongue can be wetted by the liquid in the capillary-loading process (e.g., Movie S7) and that liquid would mainly flow along the side channels that are formed between the tongue and the corolla wall. In this case, the proximal tongue hairs unfolded when the liquid flowed by, but there was still some spacing between hairs that were not loaded with the liquid (Movie S7). Hence, we assumed that the farther away a section of the tongue is from the liquid level, the less volume can be filled by capillary flow. To account for this effect, we introduced a weight function, $c_f(\tilde{x}) = a_f \tilde{x} + b_f (0 < c_f(\tilde{x}) < 1)$, for the captured liquid volume in the capillary-loading process, where \tilde{x} originates from the liquid meniscus and toward the tongue base (Fig. 3C). The coordinate \tilde{x} varies thus between 0 and $x - x_{\text{base}} = x - x_m + L_{\text{tongue}}$ and its largest value $\tilde{x} = L_{\text{tongue}}$ is obtained when $x = x_m$, i.e. when the position of the tip of the tongue coincide with the meniscus position. The weight function $c_f(\tilde{x})$ decreases linearly when \tilde{x} increases (SI Appendix, Fig. S3) and the value of its parameters a_f and b_f are determined by the boundary values at the meniscus, where we set $c_f(\tilde{x} = 0) = 100\%$ and $c_f(\tilde{x} = L_{\text{tongue}}) = 10\%$. In this case, $c_f(\tilde{x}) = 1 - 0.257 \tilde{x}$, where \tilde{x} is measured in mm. Then, the

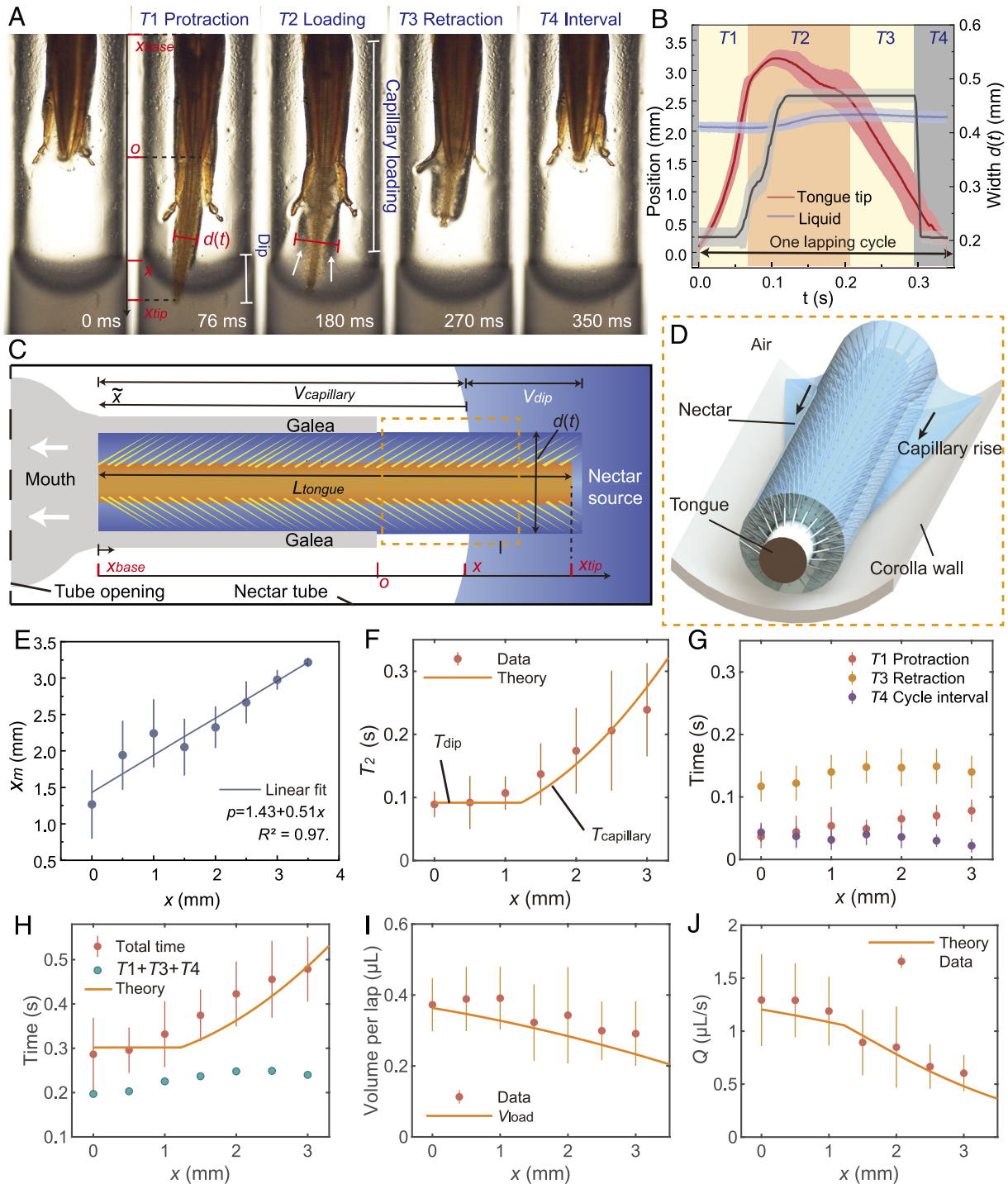


Fig. 3. Lapping mechanism of honey bees drinking in deep corolla tubes. (A) Frames from a high-speed video of a honey bee lapping deep nectar. The tip portion of the tongue can dip nectar and the rest portion of the tongue load nectar by capillarity. (B) Measured tongue tip position x_{tip} , liquid distance x , and tongue width variation $d(t)$ with respect to time in one lapping cycle when honey bees fed on 50% w/w sucrose solution ($n = 4$). T_1 , T_2 , T_3 , and T_4 denote the elapsed time in tongue protraction, liquid loading, tongue retraction, and the interval phase, respectively ($n = 5$). (C) Schematics of the tongue reaching the deep nectar kept inside the corolla tube. (D) Schematics of the tongue attached to the corolla wall and transporting nectar by capillary rise through two lateral open channels formed between the tongue and the wall. (E) Maximum tongue tip position $x_m = \text{Max}(x_{tip})$ at each lapping cycle when a honey bee laps at different liquid distances ($n = 10$). (F) Time spent in the tongue loading phase T_2 of each lapping cycle when a honey bee laps at different liquid distances ($n = 10$). (G) Elapsed time during protraction, retraction, and the interval phases across liquid distances ($n = 10$). (H) Sum of the consumed time in all four phases (orange dots) and sum of the consumed time in T_1 , T_3 , and T_4 (blue dots) of each lapping cycle across liquid distances. The curve represents the theoretical prediction of the total consumed time in one lapping cycle as a function of liquid distances. (I) Data (dots) and theoretical prediction (orange curve) of volume per lap across liquid distances ($n = 10$). (J) Lapping ingestion rate Q_{lap} ($\mu\text{L/s}$) across liquid distances ($n = 10$). For E through J, error bars are SD around averages.

volume loaded by capillarity is obtained as $V_{\text{cap}}(x) = \int_{\tilde{x}=0}^{\tilde{x}=x-x_{\text{base}}} c_f(\tilde{x}) \left((R+f_r d_m)^2 - R^2 \right) d\tilde{x}$, which fits our experimental data (Fig. 3*D*).

Finally, the lapping intake rate as a function of liquid level can be written as

$$Q_{\text{lap}} = \frac{V_{\text{load}}}{T_{\text{total}}} = \frac{V_{\text{dip}}(x) + V_{\text{cap}}(x)}{\max(T_{\text{rel}}, T_{\text{cap}}) + c} \quad [4]$$

This theoretical prediction also quantitatively agrees with the experimental data and further identifies that the feeding efficiency of honey bees lapping would be dominated by two main submechanisms or physical patterns, viscous dipping, and capillary loading.

Transition of Lapping and Sucking. We plot the theoretical expressions of the sucking rate Q_{suck} and lapping rate Q_{lap} with respect to the nectar concentrations c_s and the liquid distance x (Fig. 4*A*). The feeding method characterized by the largest ingestion rate is shown in Fig. 4*B* as a function of c_s and x . We note that suction is the preferred method to collect nectar by honey bees when the sugar concentration is low or when the distance between the liquid and the mouth is sufficiently large. When feeding 30% sucrose solution, the intersection is situated at a liquid mouth–nectar distance of around 1 to 2 mm, before which lapping yields higher feeding efficiency and after which sucking leads to faster ingestion (Fig. 4*B*). Notably, the 30% feeding experiments showed that honey bee first lapped the nectar and then switch to suction when the liquid reaches a distance of about 1.5 mm from the galea (at the meniscus depth of ~5 mm, Fig. 1*E*). The agreement with the observations supports that honey bees adjust their feeding methods according to the feeding efficiency. For feeding on 10% sucrose solutions, the low viscosity confers to the sucking method a higher efficiency at all liquid distances (Fig. 4). Contrarily, our theoretical model predicts that lapping is more efficient when ingesting 50% solution if the distance between the liquid and the galea is smaller than about 3.5 mm (Fig. 4), a value rarely achieved by honey bees. Accordingly, we rarely observe sucking when honey bees feed on very concentrated nectars regardless of its depth (Fig. 1).

Discussion

Floral nectar constitutes the main energy and water supply for honey bees (41). A single foraging trip of a honey bee may cover several kilometers (42, 43) and involve visits to hundreds of flowers (44). In nature, floral nectar does not completely reach the full capacity of each nectar reservoir because of removal by pollinators and evaporation (28). Moreover, secretion of nectar differing in volumes and concentrations may enable plants to manipulate pollinators and encourage their erratic motion from plant to plant in the interest of pollination (45). Many plants have flowers with long and thin corollas that prevent the pollinators from going inside the floral tube, keeping them feeding from a convenient place for pollen deposition and transfer (4). The energy reward is found deep inside these long corollas and when a nectarivore starts drinking, the meniscus recedes until only a thin layer of nectar is found at the bottom. Thus, the ability of the mouthparts to go inside the corolla, along with the fluid collection technique employed, will determine the profitability of floral visits. The deeper the mouthparts can reach, the wider the spectrum of flowers that pollinators can access; and the faster the collection of the liquid, the more efficient their foraging (11). We have presented here evidence that honey bees can collect nectar from deep corollas using extendable tongues, but without involving the usual lapping method, overcoming the limitation imposed by the restricted reach of their proboscis tubes.

Recent studies have examined the honey bee tongue according to its materials distribution (46), surface wettability (39), actuation mechanism, and the structural foundation of its flexibility (40), which gives us an fascinating example of how a set of structures with different material properties can be integrated to form a complex organ capable of complementary fluid capture modes. In this study, we reveal how their tongues function to collect liquid of varying viscosities concealed deep inside confined spaces. A biophysical challenge for honey bees foraging on deep corollas is that when the nectar is only reachable by the tongue tip, the portion of the hairy tongue exposed to the air may lose the capability to load nectar. We show that honey bees circumvent this natural constraint by attaching their tongues to the corolla wall, creating adjacent crevices that can host rivulets to transport nectar by active suction. Such a fluid transport strategy in nature has never been reported. Moreover, active suction and capillary loading appear to be more important mechanisms than

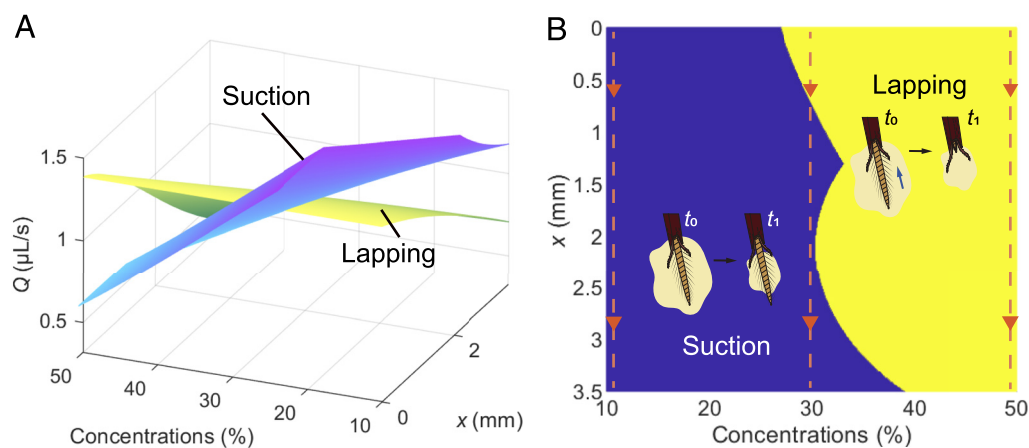


Fig. 4. Comparison of the ingestion rate between sucking and lapping patterns. (A) Comparison between the theoretical lapping and suction rates across nectar concentrations c_s and liquid distances x (mm). (B) Feeding method at different nectar concentrations and liquid distances. The blue area shows the region where $Q_{\text{suck}} > Q_{\text{lap}}$, whereas the yellow region indicates the region where $Q_{\text{lap}} > Q_{\text{suck}}$ with Q_{suck} and Q_{lap} shown in panel A. Red dashed lines highlight the feeding method against the liquid distances for nectar with 10%, 30%, and 50% sugar concentrations.

first considered for honey bees, for which dipping was the only mechanism considered for calculations of optimal concentrations in nectar feeding (5).

In addition to the skills of accommodating their feeding apparatus to reach and transport nectar, honey bees can also adjust their feeding methods in response to different nectar levels inside corollas to achieve optimal feeding efficiency. We note that the lapping-sucking transition of honey bees was previously shown to depend on nectar concentrations (24), and we now show that it depends on nectar level as well. At a nectar concentration (~30% w/w) commonly found in nature (47), honey bees can change their feeding mode as the liquid level recedes. Our observations, combined to theoretical models, illustrate that lapping at short distances can easily capture nectar to fill the tongue's maximum carrying capacity, but lapping farther away would require waiting for capillary filling, which would be less efficient than active suction. When feeding on thicker nectars (50% w/w), honey bees keep lapping but decreased their tongue back-and-forth frequency when reaching deeper inside the corolla (Fig. 1C), which suggests modulation of the frequency to allow for the capillary rise to saturate the tongue to the maximum capacity. At a high sugar concentration, lapping at all extraction depths in the corolla is a more efficient way to capture nectar, and for diluted nectars, active suction is a faster method for ingesting nectar across liquid levels (Figs. 1 and 4).

Beyond sugar concentration, many other nectar compounds, e.g., amino acids, proteins, fatty acids, salts, vitamin, secondary metabolites, and water, have currently elusive effects on the nectar viscosity and on the feeding behavior of honey bees (41), warranting further investigation. We also know little of whether other bee species show flexibility in their nectar-feeding mechanisms. Bumblebees, which have very similar tongue structures, appear to be restricted to the lapping method, both across concentrations (26) and extraction depths. Orchid bees, with an extraordinarily long proboscis, primarily suck the diluted nectar, but would sometimes show a lapping-sucking feeding mode on films (small amounts) of fluid (5, 48, 49). However, there is no report that orchid bees can adjust ingestion method according to the liquid properties or depth in the corolla. Switching, during the same feeding bout, between lapping and sucking according to the viscosity and distance of the nectar may be a unique ability allowing honey bees to be among the most abundant pollinators in the world. Our findings are relevant for research on the evolution of optimal concentrations in flowers pollinated by different taxa, on exploitative competition among pollinators, and on plant-animal coevolution, among others.

Materials and Methods

Feeding Observations. Honey bees (*Apis mellifera* L.) were sourced from two outdoor beehives kept at Sun Yat-Sen University, Guangzhou, China (23°N, 113°E). We captured workers emerging from the hives for a foraging trip and kept them in a syringe (diameter 14 mm, length 60 mm) without food for 2 h. All experiments were carried out at around 26 to 30 °C lab temperature. Since sugar (basically sucrose, glucose, and fructose) in nectar is the most essential energy source for honey bee's flight, thermoregulation, and hence and development (41), and nectar quality is commonly indicated by its sugar concentration, and hence we use sucrose solution as artificial nectar for experiments. The artificial nectar consisted of sucrose solution at three concentrations (10%, 30%, and 50% w/w). These sugar concentrations are within the range reported for natural nectar sources for bees (17). Sucrose solutions were presented in an artificial corolla made of clear glass, with an inner diameter of 1.4 mm to restrict entry of the bee's feeding organs to no more than its basal mouthparts (Movie S1). The feeding tube was horizontally set, 25 mm in length (longer than the bee proboscis), sealed at one end, and filled completely at the start of each test. We note that although the

orientation of natural floral corollas can vary from upward to downward, the small Bond number of the system (SI Appendix) implies that the gravitational effects are negligible, and the case of honey bees feeding horizontally can reasonably be used to study the global feeding mechanism. The tip of the syringe was truncated and left with a 2.5-mm opening, where we could set the corolla tube for feeding without removing the bee from the syringe. When a bee fed on the sucrose solution, we recorded the movement of its proboscis and the position of the level part of the meniscus using a camera (Canon EOS 6D Mark2, Japan) at 50 fps. We analyzed the videos by Tracker (6.0.9) and built a measurement coordinate where its origin was set at the feeding tube opening. During feeding, we tracked the time and the positions of the proboscis tube (galea tip) $x_p(t)$, tongue tip $x_{tip}(t)$, and the liquid meniscus $x_l(t)$. We define the liquid distance $x = x_l(t) - x_p(t)$ as the distance between the meniscus and the proboscis tube tip (galea tip).

According to the tongue movement and the liquid meniscus position, we can easily recognize the honey bee feeding pattern. We classify the feeding pattern as sucking if the bee ingests the nectar with tongue frequency $f < 1 \text{ s}^{-1}$, or as lapping if $f > 1 \text{ s}^{-1}$. We note that it is unlikely to give an accurate estimation of the critical tongue value between lapping and sucking, as the shift in mechanism occurs gradually by making longer and longer pauses at the end of each cycle when the tongue is at maximum protrusion (Fig. 1E). However, given that the slowest lapping frequency when honey bee feeding 50% nectar was around 2 s^{-1} , it is simple and conservative to use 1 s^{-1} as the critical value to ascertain that suction occurs. When honey bee sucks the nectar, we could recognize each pumping event (by its head pump) according to the staircase curve of liquid meniscus movement. We were able to measure the spent time $T_{suck}(x)$ and the consumed liquid volume $V_{suck}(x)$ in each pumping event during the entire feeding and then determined the averaged intake rate by $Q_{suck}(x) = V_{suck} / T_{suck}$ for each pumping event. When honey bee lapping the nectar, we could recognize each lapping event according to the tongue movements. We tracked the time and positions of the tongue tip and the corresponding meniscus position and the proboscis tube tip (galea tip) position, at the moments when 1) the tongue began to protract t_{k1} , 2) the tongue protracted out and hairs began to erect t_{k2} , 3) the tongue began to retract t_{k3} , and 4) the tongue fully retracted to the proboscis tube t_{k4} , where k denotes the k^{th} lapping cycle. Thus, we were able to derive the spent time of the tongue protraction $T_1 = t_{k2} - t_{k1}$, liquid loading $T_2 = t_{k3} - t_{k2}$, tongue retraction $T_3 = t_{k4} - t_{k3}$, and interval $T_4 = t_{(k+1)1} - t_{k4}$. The lapping rate could be determined by $Q_{lap}(x) = V_{lap} / T_{lap}$, where $V_{lap}(x)$ is the volume per lap, and $T_{lap}(x) = T_1 + T_2 + T_3 + T_4$ is the spent time per lap.

High-Speed Videography and PIV Analysis. To visualize how deep the nectar is captured by the tongue in sucking or lapping patterns, we added 5- μm microparticles (Polyamid seeding particles, Dantec Dynamics, Denmark) to the sucrose solutions (20% and 50%). The microparticles have no nutritional value for bees, and the solution with the microparticles was well accepted by bees in the experiment. The microparticles in solution have a density of 1.03 to 1.05 g / cm^3 , which is very close to the density of water, and thus, they have negligible effects on the solution density or viscosity. We set the transparent tube (diameter: 1.8 mm) under a microscope (Olympus, CX33, Japan) connected to a high-speed camera (Phantom, VEO E, USA) for recording. Since honey bees attached their tongues to the corolla wall randomly (up, down, right or left) whenever sucking or lapping, we fixed the focal distance at the upper wall of the tube. Feeding events were high-speed video recorded at 1,000 fps, and the depth of focus of the microscope objective was employed to capture clear images in the measurement plane in which the tracer particles are sharply imaged (50). We did not use a laser sheet and fluorescent particles so that we would see particles in different planes. We analyzed the high-speed images by PIV using the PIVlab toolbox in Matlab (2019a). When bees were sucking nectar, we selected the analyzed region at maximum tongue protraction and plotted the velocity vector (m/s) at this area (Fig. 2E). We also extracted the velocity component u parallel to the z direction (green dashed line, Fig. 2F), where the results indicate the maximum velocity distribution in the transverse direction. Twenty bees in total were used in the PIV analysis to examine the velocity magnitude during sucking.

Synchrotron X-ray Microimaging. We used the Synchrotron X-ray microimaging technique to visualize the internal structure of the bee head during nectar feeding. Experiments were performed at the X-ray imaging beamline BL13W at Shanghai Synchrotron Radiation Facility (Shanghai, China). An X-ray sample

detector was used to record the X-ray images (Optique Peter, PCO2000). Honey bees ($n = 10$) were kept in the syringe and fed with a 30% nectar film mixed with a diluted iodine solution on a glass slide. Feeding was recorded at 100 fps (Sony digital camera) with peak energy at 15 keV.

Data, Materials, and Software Availability. All study data are included in the article and/or [supporting information](#). The data will be accessible upon publication.

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