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This highlight refers to the PhD Thesis by Pulkit Goyal (2022)

How flying bees land

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Landing is arguably one of the most critical and difficult behaviours that flying animals regularly perform. It involves a precise control of approach speed as an animal draws closer to the landing surface. Poor control can result in high-impact collisions with the surface which can be harmful for animals. Despite its importance in flight, how animals approach a surface for landing is not yet fully understood. Here, we contribute to answering this question by examining the landing approaches of bumblebees and honeybees (Goyal, 2022). Bees, including bumblebees and honeybees, perform 100 to 1000 landings in a single hour of foraging. They perform these landings relentlessly to gather the nectar and pollen from flowers, which are essential for their survival and reproduction. We use novel real-time videography-based tracking of flying bees and dedicated control-theory-based analyses methods to investigate how these bees land.

Bumblebees land rapidly and robustly using a sophisticated modular flight control strategy

Many flying animals use visual cues during landing. In the first thesis research chapter, we present how bumblebees use visual expansion cues to advance towards the landing surface (Goyal et al., 2021). For this purpose, we first designed an indoor experimental apparatus to automatically record the landing maneuvers of foraging bumblebees using real-time videography-based tracking. Using this approach, we tracked 4,672 landing maneuvers, which we then analyzed using a novel analysis method. This method analyses the individual maneuvers and is more comprehensive than the analysis method of averaging multiple maneuvers used in literature.

Using this novel method, we discovered the visual guidance strategy of landing bumblebees. Our results show that the landing bumblebees exhibit a series of deceleration bouts during which they keep the relative rate of optical expansion approximately constant (Figure 1). This constant is referred to as a set-point and from one bout to the next, bumblebees tend to shift to a higher set-point. This newly-found guidance strategy results in the approach dynamics that is strikingly similar to that of pigeons, mallards and hummingbirds (Lee et al., 1991; Lee et al., 1993; Whitehead, 2020). In addition, we also found how bumblebees adjust this visual guidance strategy to travel faster when landing directly after a take-off than from a free-flight condition. Moreover, we also elucidated how bumblebees adjust this guidance strategy in the presence of different strength of optic expansion cues available from the landing surface (checkerboard versus spoke patterns) and different light intensities ranging from twilight to sunrise. This guidance strategy helps to explain how these important pollinators rapidly visit flowers and forage in challenging environmental conditions.

In addition to the deceleration phases, we found that landing bumblebees also occasionally exhibit low approach velocity phases ($V < 0.05$ m/s) while transitioning from one set-point to another. These low approach velocity phases are similar to the hovering phases identified in literature, and result in bumblebees hovering or sometimes even flying away from the surface for a short period. We propose that these low approach velocity phases are likely the instabilities arising out of a control system that uses optical expansion rate as a control variable.

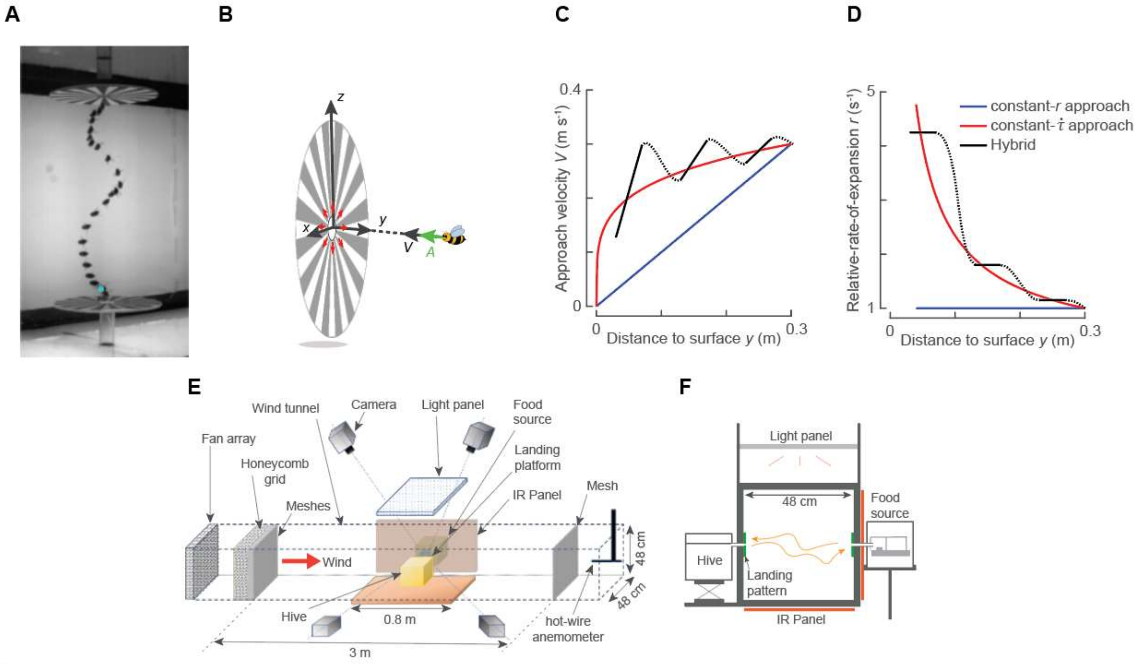

Figure 1 – The experimental set-up developed in this thesis, and the landing strategies described in honeybees (blue), birds (red) and bumblebees (black). (A) Photomontage from a downward-facing camera of a landing bumblebee, at a time interval of ~0.1 s. (B) An animal that approaches a vertical landing platform along its axial direction experiences a relative optical expansion rate as symbolized by the red arrows. At time t, the animal is at distance y from the object, has an approach flight velocity V, experiences a relative-rate-of-expansion of r=V/y, and has an instantaneous time-to-contact τ=y/V. (B,C) The variation with distance from the landing surface of (B) approach velocity V, and (C) relative-rate-of-expansion r, for the constant-r landing approach observed in honeybees (blue) (Baird et al., 2013), the constant-τ̇ landing approach of birds (red) (Lee et al., 1991; Lee et al., 1993; Whitehead, 2020), and the here-described hybrid landing approach of bumblebees (black) (Goyal et al., 2021). The hybrid landing approach consists of constant-r segments (solid lines), separated by transition phases (dotted curves). All results, and particularly the transition phases, are of idealized cases. (E,F) Our experimental setup consisted of a wind tunnel with two vertically placed circular landing surfaces connected to a hive and a food-source, respectively. Foraging bumblebees that flew between these landing surfaces were tracked in real-time using a four-camera videography system. Visible and IR LED light panel were used for background illumination and for videography, respectively.

Bumblebees land rapidly by intermittently accelerating and decelerating toward the surface during visually guided landings

For achieving a goal such as evading a threat or reaching a set-point, animals use their sensorimotor control system to continuously parse the sensory information and change the wingbeat and body kinematics to produce the required forces and torques. In the second thesis research chapter, we focused on the sensorimotor control system that landing bumblebees use to execute their visual guidance strategy (Goyal et al., 2022). We used the natural stepwise excitation that landing bumblebees offer to analyze how their different subsystems (sensory system, controller and motor system) function together to reach the set-points of optical expansion rate. Our results showed that their closed-loop sensorimotor control system regulates the relative rate of expansion during landing. The track segments before and during a set-point are the transient and steady-state responses of such a control system. Bumblebees use the transient response to mostly accelerate and steady-state response to always decelerate during their landing approach. We also identified how the transient response varies among the tested environmental conditions (light intensity and the strength of optic expansion cues) and starting conditions (landings from a free-flight or after a take-off). Based on these results, we propose a sensorimotor control system of landing bumblebees that facilitates a rapid and robust execution of their visual guidance strategy (Figure 2a).

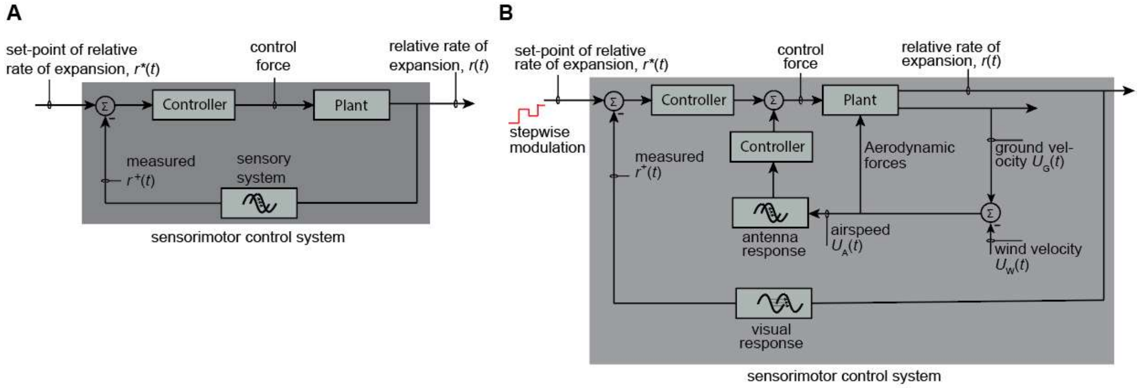

Figure 2 –The sensorimotor control system of landing bumblebees. (A) The closed-loop sensorimotor control system that landing bumblebees use to converge the optical expansion rate r to a set-point r. Using their visual system, bumblebees measure optical expansion rate as r+. Based on the difference between r+ and r*, the animal produces a proportional aerodynamic control force, which accelerates the animal ("plant" in control terminology). (B) The multimodal sensory integration model of landing bumblebees that explains the transient dynamics observed in the presence of steady sidewinds. Bumblebees use their antennae to measure the wind-induced mechanosensory input (airspeed) and integrate it with positive feedback in their vision-based sensorimotor control loop. This fast positive feedback can provide active damping that counteracts the unstable oscillations of a visual feedback loop.*

Bumblebees actively compensate for the adverse effects of sidewind during visually-guided landings

Bumblebees regularly experience winds during foraging. The winds in nature can be characterized as mean winds and fluctuations around them. In the third thesis research chapter, we investigated how the mean winds affect the visual guidance strategy, the sensorimotor control system and the landing performance of foraging bumblebees (Goyal, 2022). For this, we developed a wind tunnel in which bumblebees could forage by flying from one side of the tunnel to the other, and thereby experience a constant side wind (Figure 1E,F). Hereby, we used six steady sidewinds ranging from 0 to 3.4 m/s, which are sidewinds that foraging bumblebees naturally encounter.

We found that the visual guidance strategy and the sensorimotor control response of bumblebees in these wind conditions is similar to the still-air response, but bumblebees exhibit some important adaptations in winds. Compared to the still-air situation, bumblebees more often exhibit low approach velocity phases in higher wind speeds. This can lead to an increase in the travel time and hence, can adversely affect their foraging efficiency. But, bumblebees also exhibit faster transient responses and higher set-points with increasing wind speed which enable them to travel faster. This in turn allows bumblebees to compensate for the increase in travel time that would otherwise occur due to more low approach-velocity phases in higher winds.

In addition to revealing the adverse effects of winds and the compensation mechanism of bumblebees during landing, we also use the natural excitation of the sensorimotor control system that bumblebees offer during landing to propose how they integrate information from the airspeed measuring mechanosensors with their visual feedback loop (Figure 2b).

Visual guidance of landing approaches in honeybees

In the fourth thesis research chapter, we revise the visual guidance strategy of landing honeybees previously proposed in literature (Goyal, 2022). In literature, honeybees are shown to linearly decrease their approach velocity with the reducing distance by analyzing the average of multiple landing maneuvers (Baird et al., 2013). Based on this result, it has been suggested that they land by holding the relative rate of optical expansion constant throughout their approach. We use the novel analysis technique developed in this thesis to show that the individual honeybees do not follow such a strategy. They instead stepwise modulate their set-point of optical expansion rate during landing. Moreover, we extend the analysis to find the mechanism that allows honeybees to converge to a stereotypic landing maneuver closer to the landing surface, for a large range of initial flight speeds and visual landing platform patterns. Finally, we compare the landing strategies of bumblebees and honeybees found in this thesis (Figure 3) and elucidate the likely causes of the differences between their strategies.

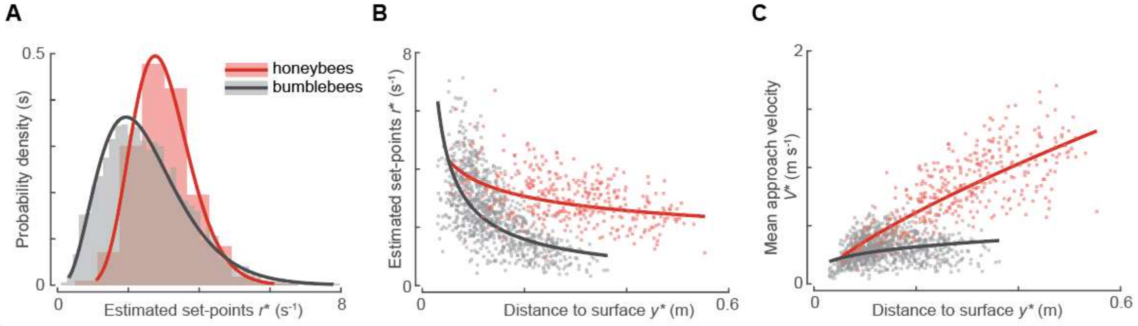

Figure 3 – Comparison of the landing strategies observed in honeybees (red) and bumblebees (grey). (A) The probability density of the set-points of relative rate of expansion r for the landings of honeybees (red) and bumblebees (grey). (B,C) The set-points of relative rate of expansion r* (B) and the mean approach velocity V* (C) with mean distance to the landing platform y*, for honeybees (red) and bumblebees (grey) as they approached a landing surface. Note that the solid lines in panels (B) and (C) also correspond to the theoretical curves that would result from following the constant time-to-contact-rate $\dot{\tau}$ landing strategies suggested in birds (Lee et al., 1991; Lee et al., 1993; Whitehead, 2020).*

Visual guidance and sensorimotor control of landing maneuvers in bees

Considering all results together, in this thesis we developed and used a novel analysis to demonstrate that bumblebees and honeybees have evolved a sophisticated flight control strategy to execute rapid landings. Moreover, we have shown that they have evolved ways to adjust this modular guidance strategy to deal with the challenges offered by the environment, such as high sidewinds.

References

Baird, E., Boeddeker, N., Ibbotson, M. R. and Srinivasan, M. V., 2013. A universal strategy for visually guided landing. Proc. Natl. Acad. Sci. 110, 18686–18691.

Goyal, P., 2022. How bees land. PhD Thesis, Wageningen University & Research.

Goyal, P., Cribellier, A., de Croon, G. C. H. E., Lankheet, M. J., van Leeuwen, J. L., Pieters, R. P. M. and Muijres, F. T., 2021. Bumblebees land rapidly and robustly using a sophisticated modular flight control strategy. iScience 24, 102407.

Goyal, P., van Leeuwen, J. L. and Muijres, F., 2022. Bumblebees Land Rapidly by Intermittently Accelerating and Decelerating Towards the Surface During Visually Guided Landings. iScience 25, 104265.

Lee, D. N., Reddish, P. E. and Rand, D. T., 1991. Aerial docking by hummingbirds. Naturwissenschaften 78, 526–527.

Lee, D. N., Davies, M. N. O., Green, P. R. and (Ruud). Van Der Weel, F. R., 1993. Visual control of velocity of approach by pigeons when landing. J. Exp. Biol. 180, 85–104.

Whitehead, J. G., 2020. An examination of the kinematics and behavior of mallards (Anas platyrhynchos) during water landings.