# Evidence for ventral optic flow regulation in honeybees

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# EVIDENCE FOR VENTRAL OPTIC FLOW REGULATION IN HONEYBEES

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**ABSTRACT**
To better grasp the visuomotor control system underlying insects' height and speed control, we attempted to interfere with this system by producing a major perturbation on the free flying insect and obsering the effect of this perturbation. Honeybees were trained to fly along a high-roofed tunnel, part of which was equipped with a moving floor. The bees followed the stationary part of the floor at a given height. On encountering the moving part of the floor, which moved in the same direction as their flight, honeybees descended and flew at a lower height. In so doing, bees gradually restored their ventral optic flow (OF) to a similar value to that they had perceived when flying over the stationary part of the floor. OF restoration therefore relied on lowering the groundheight rather than increasing the groundspeed. This result can be accounted for by the control system called an *optic flow regulator* that we proposed in previous studies. This visuo-motor control scheme explains how honeybees can navigate safely along tunnels on the sole basis of OF measurements, without any need to measure either their speed or the clearance from the ground, the roof or the surrounding walls.

**KEY WORDS**
Optic flow, insect flight, collision avoidance, visuo-motor control system.

## 1. Introduction

Flying insects are able to navigate in unfamiliar environments by relying on the *optic flow* (OF) ([1], [2]) that is generated by their own translation over contrasting objects ([2], [3], [4], [5], [6]). They rely on OF cues to avoid obstacles ([7], [8], [9]), to control their speed ([10], [11], [12], [13], [14], [15], [16]), to control their height, and to land ([12], [14], [17], [18], [19], [20]).
Recent studies have confirmed that the ventral OF plays a particular role in honeybees' flight control processes ([12], [14], [15], [19]). The latter authors used various tunnels, the floor of which was lined with stationary patterns of various kinds, such as 2-D patterns providing many ventral OF cues, axial patterns providing few ventral OF cues or a homogeneous pattern providing hardly any OF cues. Honeybees were found to fly on average at a lower height and a higher speed when only few ventral OF cues were available ([14], [15]).

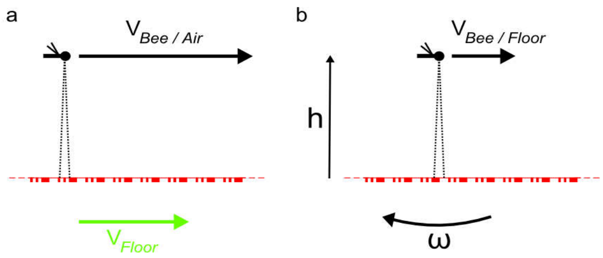


Fig 1. (a) The bee was flying at an airspeed of $V_{Bee/Air}$, which was equal to the ground speed since there was no wind. However, the floor could be set in motion at speed $V_{Floor}$ in the same direction as the flight. The bee's speed relative to the floor $V_{Bee/Floor}$ is therefore given by: $V_{Bee/Floor} = V_{Bee/Air} - V_{Floor}$. (b) The ventral OF perceived in the vertical downward direction by the bee flying at height h and speed $V_{Bee/Floor}$ is the angular speed defined as $\omega = V_{Bee/Floor} \div h_{Bee/Floor}$ [rad/s].

In the outdoor experiments described here ([21]), free flying honeybees were deliberately subjected to a major step perturbation in their ventral OF, using a moving floor lined with transverse contrasting patterns set in motion at constant speed in the same direction as the flight (Fig. 1a, b). The bees' behavior was quantified in terms of their individual trajectories in the vertical (longitudinal) plane and statistical analyses were performed on the data obtained.

## 2. Materials and methods

Flight tunnel

The floor, the high roof and the left wall of the outdoor flight tunnel (220-cm long, 100-cm high and 25-cm wide) consisted mainly of planks lined with printed red and white stripes. The right wall consisted of a thin white insect netting lined with stripes consisting of a red gelatin filter (Lee Filters HT019), through which the honeybees' flight paths could be seen and video-recorded. Part of the floor (between abscissa $x$ = 60 cm and $x$ = 210 cm) consisted of a 25-cm wide belt printed with the same red and white pattern, stretched between two drums. A speed regulated, brushless motor coupled to one of the drums drove the belt at a speed of 0–140 cm/s. The tunnel was closed with a white plank at each end. Two openings (5 * 5 cm) placed 10 cm above the floor gave the bees entry to the tunnel and access to the reward, respectively. They were opened and closed manually by the experimenter. The outdoor flight tunnel was oriented to the north and received only indirect illumination (no direct sunlight).

Pattern

The patterns consisted of red and white stripes oriented perpendicularly to the direction of flight. These red stripes had two different widths (1 cm and 3 cm) and formed a simple 10 cm-wide pattern that was repeated regularly, as shown in figure 1. The angular subtends of the stripes ranged from 5.7° to 53° (1–10 cm wide pattern viewed from a distance of 10 cm, respectively) and from 0.5° to 5.3° (1–10 cm-wide pattern viewed from 1 m, respectively). The Michelson contrast between the red and white stripes was $m = 0.47$ on the planks and $m = 0.25$ on the insect netting. A red filter placed in front of the camcorder monitoring the honeybees' trajectories (through the insect netting) made it possible to optimize the contrast between the insect and the background.

Experimental procedure

Groups of four to six freely flying honeybees (*Apis mellifera*) were marked and trained outdoors to enter the tunnel and fly along it to collect sugar solution at the opposite end. During the training phase, the floor was always kept stationary. Once bees had received about 30 rewards, their flight path was recorded with the digital camera from the insect-netting side, on their way to the (expected but fictive) reward. Only one bee at a time was recorded under two conditions: (1) stationary floor and (2) floor set in motion in the same direction as the honeybees' flight, at a speed of 0.5 m/s. The two experimental conditions were balanced to prevent any effects of prior exposure to ventral OF disturbances on the subsequent flight path. The camcorder and the floor motion were triggered at the moment when the honeybee entered the corridor. During the recordings, the white door giving access to the reward remained seamlessly closed to rule out the presence of any uncontrolled attractive cues.

Video recordings and flight path analysis

The honeybees' trajectories were filmed at a rate of 20 frames per second (Ts = 50 ms) with a high-resolution black-and-white CMOS camera (Prosilica EC1280). The camera was placed sideways, 2.3 m from the insect netting. The field of view extended over the entire tunnel height (100 cm), from abscissa $x$ = 20 cm to abscissa $x$ = 180 cm. In both experimental conditions, the bees first flew over the stationary part of the floor (from $x$ = 0 cm to $x$ = 60 cm), and then over the longer part (150 cm) that could be either kept stationary or set in motion (from $x$ = 60 cm to $x$ = 210 cm). Image sequences were processed using ImageJ macros and analyzed using the Matlab script program to determine the bee's flight height ($h$) as a function of the abscissa ($x$) along the tunnel axis in each frame. Each trajectory was mapped, based on the successive ($x$, $h$) positions of the bee. The airspeed of each trajectory was computed at each abscissa $x$, using a four-point derivative smoothing filter ($V_{Bee/Air}(t) = (2x_{Bee}(t - 2) + x_{Bee}(t - 1) - x_{Bee}(t + 1) - 2x_{Bee}(t + 2))/10Ts$).

Statistical analysis

The parameters used in the analysis were the bee's airspeed ($V_{Bee/Air}$), the bee's speed with respect to the floor ($V_{Bee/Floor}$) and the floor speed ($V_{Floor}$). $V_{Bee/Floor}$ was obviously obtained by subtracting $V_{Floor}$ from $V_{Bee/Air}$ : $V_{Bee/Floor} = V_{Bee/Air} - V_{Floor}$.
All the individual trajectories recorded have been plotted in figure 2a, b. The histograms on the right were computed using the average flight height of individual honeybees between $x$ = 60 cm and $x$ = 180 cm. A paired sample $t$-test was used to compare the means of the

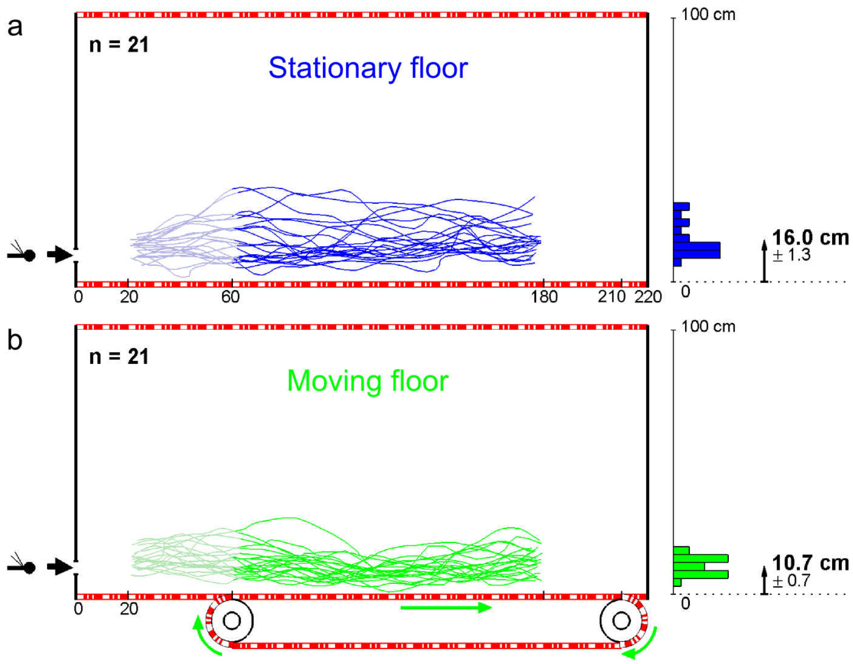


Fig. 2. Side view of the trajectories of 21 individual honeybees flying freely along the tunnel under two conditions: (a) over a stationary floor, and (b) over a floor part of which moved in the same direction as the bees. The horizontal visual field of the camera (20 cm * 180 cm) covered the transition between the stationary and moving parts of the floor. The latter extended up to $x$ = 210 cm. The blue trajectories were recorded over the stationary floor, and the green trajectories over the part of the floor set in motion. All error bars are ±SEM. (a) When the floor was stationary, the honeybees flew at a height of 16 ± 1.3 cm above the floor. (b) When the floor was set in motion (at a speed of $V_{Floor}$ = 0.5 m/s) in the same direction as the honeybees' flight, the insects descended and flew at a height of only 10.9 ± 0.7 cm above the floor.

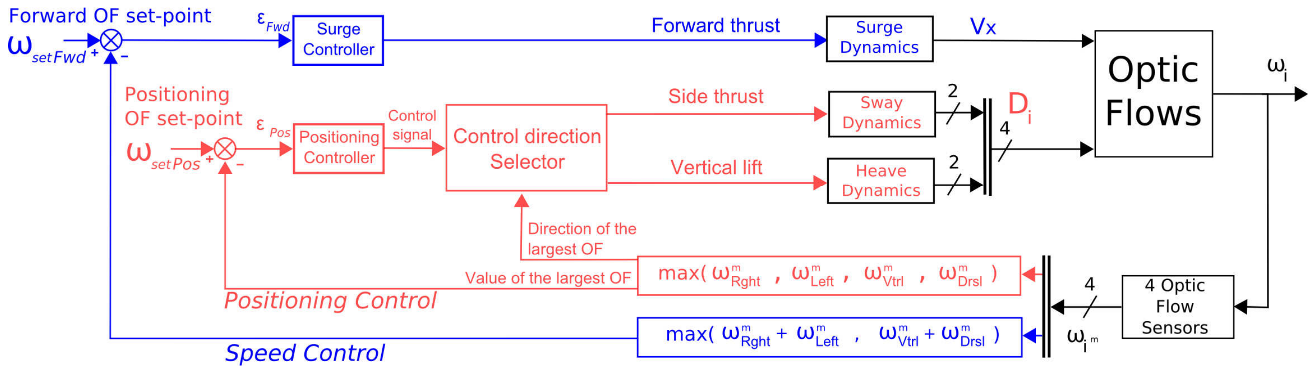


Fig. 3. The ALIS autopilot ([22]) is based on two interdependent visual feedback loops, each with its own OF set-point: a speed control loop (in blue) and a positioning control loop (in red). The surge controller adjusts the pitch angle $\theta_{pitch}$ (that determines $V_x$ via the bees' surge dynamics) on the basis of whichever sum ("left OF + right OF" or "dorsal OF + ventral OF") of the two coplanar OFs measured is the larger. This value is compared with the forward OF set-point $\omega_{setFwd}$. The surge controller commands the forward speed so as to minimize the error $\varepsilon_{Fwd}$. The positioning controller controls the roll angle $\theta_{roll}$ (or the stroke amplitude $\Delta\varphi$), which determines the distances to the walls (or the distances to the ground and to the roof), depending on the sway (or heave) dynamics, on the basis of whichever of the four measured OFs is the largest. The latter value is compared with the positioning OF set-point $\omega_{setPos}$. At any time, the direction of avoidance is given by a Control direction Selector that multiplies the control signal by a direction factor depending on the direction of the maximum OF signal. The positioning controller commands the sway (or heave) dynamics so as to minimize the error $\varepsilon_{Pos}$. The dash across the connection lines indicates the number of variables involved. $D_i$ is the distance to the surface involved.

averaged individual flight heights.
All error bars are given as ± standard error of the mean (SEM).

## 3. Results

Figure 2 shows the two side views of all the honeybees' trajectories obtained in the two conditions: with a stationary floor (Fig. 2a), and with the floor steadily moving in the same direction as the bee, at the speed $V_{Floor}$ = 0.5 m/s (Fig. 2b). Over the initial, stationary part of the floor (i.e., up to $x$ = 60 cm), honeybees flew at virtually the same height in both conditions (14.8 ± 1.1 cm and 13.6 ± 0.9 cm, respectively, $df$ = 38.3, $p$ = 0.44). Over the mobile part of the floor, bees descended conspicuously when the floor moved at 50cm/s and flew at a lower height on average (10.7 ± 0.7 cm vs. 16 ± 1.3 cm, $df$ = 30.1, $p$<0.01) (Fig. 2b). The result obtained was therefore that moving the floor in the flight direction forced the honeybees to descend and fly closer to the ground.

## 4. Conclusion

The present findings ([21]) can be said to provide the most direct evidence available to date on height control in honeybees. The data obtained here reveal that honeybees attempt to maintain their ventral optic flow (OF) constant by altering their flight height rather than their flight speed and that they keep doing so when their control system is subjected to a major ventral OF perturbation, such as that induced by the artificially triggered movement of the floor. This is in line with previous findings made in various flight tunnels, the floors and sides of which were lined with variously contrasting patterns ([12], [13], [14], [15], [19]). Moreover, the findings presented here are perfectly in line with the *OF-regulator* control scheme piloting height, which accounted for a host of disparate flight patterns observed in various insect species during the last 70 years [20]. The enhanced control system (ALIS, Fig. 3) that we recently came up with ([22]) suggests that the bees' vertical and horizontal positions may be piloted by one OF regulator, while their airspeed is piloted by another OF regulator. The first one uses the *largest* OF perceived (left, right, ventral or dorsal) to pilot the bees' vertical and horizontal positions and the second one uses the *larger sum* of the opposite OFs (''left OF + right OF'' or ''ventral OF + dorsal OF'') to pilot the airspeed. This model ([22]) is also consistent with the results of previous behavioural studies ([9], [12], [15], [19], [23]).
In the context of insects' autopilots, the great advantage of the ALIS dual OF-regulator is that it makes an insect automatically select both a safe speed and a safe clearance, without any need for onboard speed sensors or range sensors. This provides for a new, minimalist and much cheaper way of piloting an aircraft or a spacecraft, provided there are photons and contrasting features in the environment ([24], [25]).
Further behavioral experiments are now required to challenge this autopilot model and further improve our understanding of honeybees' flight control systems.


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## References

[1] J.J. Gibson, The perception of the visual world, Boston: *Houghton Mifflin*, 1950.

[2] J.S. Kennedy, The migration of the desert locusts (Schistocerca gregaria Forsk), *Phil. Trans. Roc. Soc. Lond. B*, *235*, 1951, 163-290.

[3] C.T. David, Height control by free-flying Drosophila, *Physiol. Entomol.*, *4*, 1979, 209-216.

[4] C.T. David, Compensation for height in the control of groundspeed by Drosophila in a new 'Barber's pole' wind tunnel. *J. Comp. Physiol. A*, *147*, 1982, 485-493.

[5] G.A. Horridge, The evolution of visual processing and the construction of seeing system, *Proc. Roy. Soc. Lond. B*, *230*, 1987, 279-292.

[6] G.K. Taylor, and H.G. Krapp, Sensory systems and flight stability: what do insects measure and why?, *Adv. Insect Physiol.*, *34*, 2008, 231-316.

[7] W.H. Kirchner, and M.V. Sinivasan, Freely flying honeybees use image motion to estimate object distance, *Naturwissenschaften*, *76*, 1989, 281-282.

[8] M.V. Srinivasan, M. Lehrer, W.H. Kirchner, and S.W. Zhang, Range perception through apparent image speed in freely flying honeybees, *Vis. Neurosci.*, *6*, 1991, 519-535.

[9] J. Serres, F. Ruffier, G.P. Masson, and N. Franceschini, A bee in the corridor: centering or wall-following?, *Naturwissenschaften*, *95*, 2008, 1181-1187.

[10] R. Preiss, and E. Kramer, Control of flight speed by minimization of the apparent ground pattern movement, in Localization and orientation in biology and engineering (*D. Varju*, *Schnitzler*, *Springer*, *Berlin*, 1984, 140-142)

[11] R. Preiss, Motion parallax and figural properties of depth control flight speed in an insect, *Biol. Cyb.*, *57*, 1987, 1-9.

[12] M.V. Srinivasan, S.W. Zhang, M. Lehrer, and T.S Collett, Honeybee navigation. en route to the goal: visual flight control and odometry, *J. Exp. Biol.*, *199*, 1996, 237-244.

[13] E. Baird, M.V. Srinivasan, S. Zhang, and A. Cowling, Visual control of flight speed in honeybees, *J. Exp. Biol., 208*, 2005, 3895-3905.

[14] E. Baird, M.V. Srinivasan, S. Zhang, R. Lamont, and A. Cowling, Visual control of flight speed and height in honeybee, *LNAI*, *4095*, 2006, 40-51.

[15] A. Barron, and M.V. Srinivasan, Visual regulation of ground speed and headwind compensation in freely flying honey bees (*Apis mellifera*), *J. Exp. Biol.*, *209*, 2006, 978-984.

[16] S.N. Fry, N. Rohrseitz, A.D. Straw, and M.H. Dickinson, Visual control of flight speed in *Drosophila melanogaster*, *J. Exp. Biol.*, *212*, 2009, 1120-1130.

[17] L.P.S. Kuenen, and T.C. Baker, Optomotor regulation of ground velocity in moths during flight to sex pheromone at different heights, *Physiol. Enthomol.*, *7*, 1982, 193-202.

[18] H.Y. Fadamiro, T.D. Wyatt, and M.C. Birch, Flying beetles respond as moth predict: optomotor anemotaxis to pheromone plumes at different heights, *J. Insect Behav.*, *11*, 1998, 549-557.

[19] M. V. Srinivasan, S.W. Zhang, J.S. Chahl, E. Barth, and S.Venkatesh, How honeybees make grazing landings on flat surfaces, *Biol. Cyb.*, *83*, 2000, 171-183.

[20] N. Franceschini, F. Ruffier, and J. Serres, A bio-inspired flying robot sheds light on insect piloting abilities, *Current Biology*, *17*, 2007, 329-335.

[21] G. Portelli, F. Ruffier, and N. Franceschini, Honeybees change their height to restore their optic flow, *J. Comp. Physiol. A*, *196*, 2010, 307-313.

[22] G. Portelli, J. Serres, F. Ruffier, and N. Franceschini, Modelling honeybee visual guidance in a 3-D environment, *J. Physiol. Paris, 104*, 2010, 27-39.

[23] J. Serres, D. Dray, F. Ruffier, and N. Franceschini, A vision-based autopilot for a miniature air-vehicle : joint speed control and lateral obstacle avoidance, *Auton. Rob.*, *25*, 2008, 103-122.

[24] N. Franceschini, Toward automatic visual guidance of aerospace vehicles: from insects to robots. *Acta Futura*, *3*, 2009, 15-34.

[25] F. Valette, F. Ruffier, S. Viollet, and N. Franceschini, Biomimetic optic flow sensing applied to a lunar landing scenario, *Proc. of IEEE International Conference on Robotics and Automation*, 2010, 2253-2260.