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Aerial navigation and optic flow sensing: a biorobotic approach

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Abstract

This chapter addresses some of the control problems involved in animal's visually guided 3D piloting. We formulated explicit control schemes which explain how insects may navigate *without requiring any distance or speed measurements*. The concept of the *optic flow regulator*, a feedback control system based on *optic flow sensors*, is presented. Based on a number of behavioral experiments conducted in our laboratory and elsewhere, we explain how *OF regulators* suffice to account for various insect flight patterns observed over the ground and over still water, under calm and windy conditions, and in straight or tapered corridors. These control schemes were tested in simulation and implemented onboard two types of insect-like robots, a micro-helicopter and a micro-hovercraft, which behaved very much like insects when placed in similar environments. These robots were all equipped with electro-optic OF sensors inspired by the results of our previous microelectrode studies on the motion sensitive neurons present in the flies' eyes. The simple and parsimonious control schemes described here do without any conventional avionic devices such as radio-altimeters, laser rangefinders, variometers, radars, sonars or GPS receivers. While these control schemes are little demanding in terms of neural resources - consistent with their integration in the less-than-one-milligram insect's brain - they show great potential for simplifying the design of aerial and space vehicles, with interesting prospects in weight-reduction and low consumption.

Introduction

Insects are no more that kind of dumb creatures they used to be. Some insects have well developed learning and memory capacities whose essential mechanisms do not differ drastically from those of vertebrates (Giurfa and Menzel, 1997, Giurfa, 2003). Flying insects have been in the business of sensory-motor integration for more than hundred millions years. These star pilots navigate swiftly through most unpredictable environments, often attaining a level of agility that greatly outperforms that of both vertebrate animals and present day aerial robots. Insects are capable of dynamic stabilization, 3D autonomous navigation, ground avoidance, collision avoidance with stationary and nonstationary obstacles, tracking, docking, decking on movable substrates, autonomous takeoff, hovering, landing, etc. They also behave in a predictive manner, making the appropriate anticipatory postural adjustments that will allow them to take off in the right direction when they notice an approaching threat (Card and Dickinson, 2008).

Insects' neural circuits are highly complex - commensurate with the sophisticated behavior they mediate - but unlike most (no less complex) vertebrate neural circuits, they can be investigated at the level of single, *uniquely identifiable neurons*, i.e., neurons that can be reliably identified in all the individuals of the species on the basis of their location in the ganglion, their exact shape and their consistent electrical responses. This great advantage of insect versus vertebrate neuroscience enables insect neuroscientists to accumulate knowledge during anything from a few days to several decades about a given individual neuron or a well defined neural circuit (Strausfeld, 1976, Hausen and Egelhaaf, 1989, Frye and Dickinson, 2001).

This chapter deals with the autopilot systems that may allow insects to fly safely without bumping into things. The chapter summarizes our recent attempts to formulate explicit control schemes explaining how insects may navigate *without requiring any distance or speed measurements*. The aim of these studies was not to produce a detailed neural circuit but rather to obtain a picture that abstracts some basic control laws. We attempted to determine the variables the insect needs to measure, the variables it needs to control, and the causal and dynamic relationships between the sensory and motor variables involved.

The last decades have provided evidence that flying insects guide themselves visually by processing the *optic flow* (OF) that is generated on their eyes as a consequence of their locomotion. In the animal's reference frame, the translational OF is the *angular speed* ω at which contrasting objects in the environment move past the animal as a consequence of locomotion (Kennedy, 1939; Gibson, 1950; Lee, 1980; Koenderink, 1986).

Our progress was achieved by performing simulation experiments and testing our control schemes onboard miniature aerial robots. Constructing a bio-inspired robot first requires exactly formulating the signal processing principles at work in the animal. It gives us, in return, a unique opportunity of checking the soundness and robustness of those principles by bringing them face to face with the real physical world (see also Webb, 2001).

Like the early terrestrial Robot-Fly (the "robot-mouche": Pichon et al., 1989; Franceschini et al., 1992), our aerial robots are based on the use of electronic *OF sensors* (Blanes, 1986, Franceschini et al., 1986) inspired by the housefly Elementary Motion Detectors (EMDs), which we previously studied in our laboratory (Rev.: Franceschini, 1985, 1992; Franceschini et al., 1989).

After recalling some aspects of the fly visual system and its motion sensitive neurons, we focus on the realisation of fly-inspired OF sensors. We then examine the problem of ground avoidance by flying creatures and introduce the principle of OF regulation. The micro-helicopter demonstrator we built is then described, equipped with an electronic *OF sensor* and an *OF regulator*. The extent to which the *OF regulator* concept accounts for the actual

behavioral patterns observed in insects is discussed. The results of recent behavioral experiments on honeybees trained to enter a corridor led us to introduce the *dual OF regulator*, an OF-based autopilot that is able to control both speed and clearance from the walls. This autopilot's performance was tested in simulation on a micro-hovercraft. We conclude by discussing the potential applications of these insect-derived principles to the navigation of aerial vehicles - in particular Micro Aerial Vehicles (MAVs) and Micro Space Vehicles (MSVs) which, like insects, are not supposed to carry the prohibitively large sensors and control systems present on conventional aircraft.

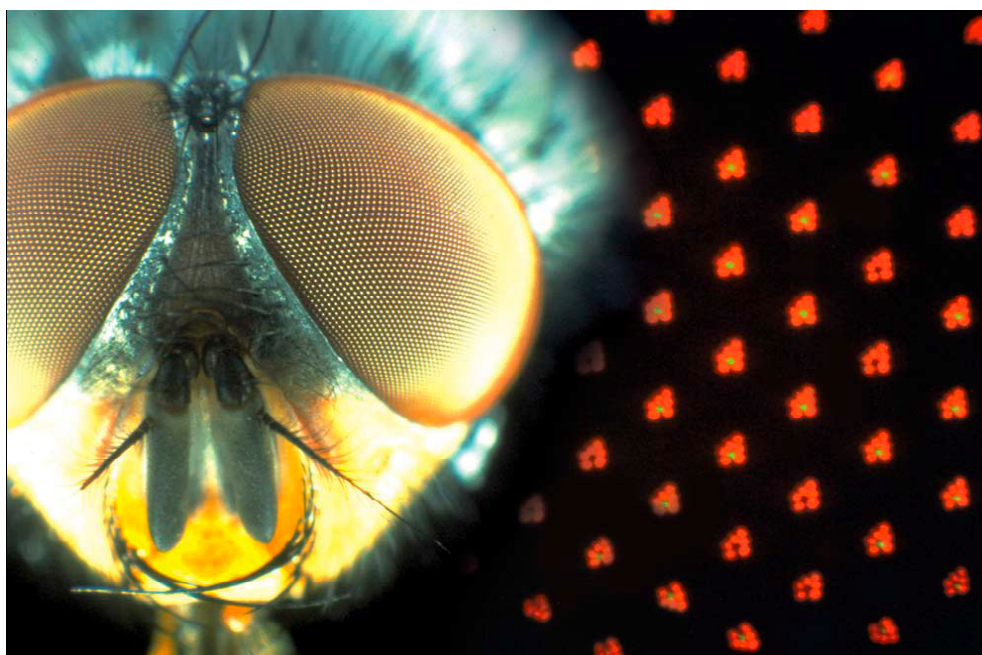


Figure 1: Head of the blowfly *Calliphora erythrocephala* with its panoramic compound eyes (left). The right part shows about 2% of the housefly retinal mosaic. A cluster of micrometer-sized photoreceptors is located in the focal plane of each facet lens : 6 outer receptors R1-6 surround a central cell R7 (prolonged by an R8, not seen here). These are the natural *autofluorescence* colors of the receptors observed *in vivo* under blue excitation (Franceschini et al., 1981a,b), after “optical neutralization of the cornea” (Franceschini, 2007).

The fly visual system and its motion sensitive neurons

Each compound eye consists of an array of *ommatidia*, the frontend of which is a facet lens that focusses light on a small group of photoreceptor cells (Fig.1, right). The fly retina is among the most complex and best organized retinal mosaic in the animal kingdom. It has been described in great details, with its different spectral types of photoreceptor cells, polarization sensitive cells and sexually dimorphic cells. There exists a typical *division of labour* within the retina (Rev.: Franceschini, 1984, 1985; Hardie, 1985):

- The two central photoreceptor cells, R7-8, display various spectral sensitivities that are randomly scattered across the retinal mosaic, as attested by the characteristic R7 autofluorescence colors (Fig. 1). R7 and R8 are thought to participate in *color vision*.

- The outer 6 photoreceptor cells (R1-R6) all have the same, dual-peak spectral sensitivity (blue-green + UV). They participate, in particular, in *motion detection* (Rev.: Buchner, 1984, Heisenberg and Wolf, 1984; Riehle and Franceschini, 1984). In this visual pathway, signal-to-noise ratio is improved by the presence of an ultraviolet sensitizing

pigment that enhances their quantum catch (Kirschfeld et al., 1977), and by an exquisite opto-neural projection called *neural superposition* (Braitenberg, 1967; Kirschfeld, 1967; Kirschfeld and Franceschini, 1968). The R1-R6 photoreceptors therefore make for a high sensitivity (“scotopic”) system (Kirschfeld and Franceschini, 1968).

To estimate the OF, insects use *motion sensitive neurons*. Flies analyze the OF locally, pixel-by-pixel, via a neural circuit called an “Elementary Motion Detector” (EMD). Further down the neural pathways, more precisely in that part of the third optic ganglion called the lobula plate (LP), about 60 large-field collator neurons called “lobula plate tangential cells“ (LPTCs) integrate the outputs of large numbers of EMDs (Rev.: Hausen and Egelhaaf, 1989; Egelhaaf and Borst, 1993; Hausen, 1993). The LPTC neurons analyze the OF field generated by the animal’s locomotion (Rev.: Krapp et al., 1998; Borst and Haag, 2002, Taylor and Krapp, 2008). Some of them transmit electrical signals via the neck to thoracic interneurons directly or indirectly responsible for driving the wing-, leg-, or head-muscles. Other LPTCs (in particular, the H1 neuron, Fig.2b) send relevant signals to the contralateral eye. Taking advantage of the micro-optical techniques we had developed earlier (Rev.: Franceschini, 1975), we were able to activate a single EMD in the eye of the living housefly by stimulating single *identified* photoreceptor cells within a single ommatidium while recording the response of an *identified* motion sensitive neuron (H1) in the LP (Riehle and Franceschini, 1984, Franceschini, 1985, 1992 ; Franceschini et al., 1989).

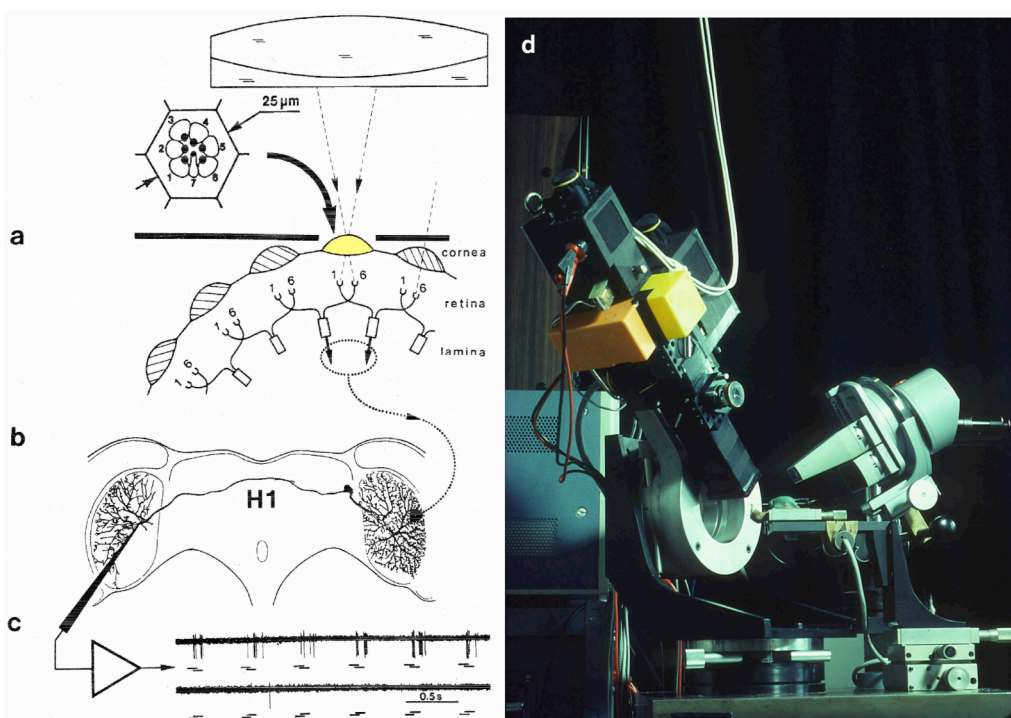


Figure 2: (a-c) Principle of the experiment aimed at deciphering the principle of motion vision in flies, using optical stimulation of single photoreceptors. (d) Triple-beam incident light “microscope-telescope” that delivers a $1\mu\text{m}$ light spot to two neighboring photoreceptor cells, R1 and R6, *successively* (see (a)). A microelectrode (c) records the unit response (nerve impulses) of the motion sensitive neuron H1 to this “apparent motion” (Franceschini et al., 1989).

We applied pinpoint stimulation to two neighboring photoreceptors (diameter $\cong 1\mu\text{m}$) within the selected ommatidium (Fig.2a) by means of a high-precision instrument (a hybrid between a microscope and a telescope: figure 2d), where the main objective lens was a single ocular

facet (diameter $\cong 25\mu\text{m}$, focal length $\cong 50\mu\text{m}$). This laboratory-made optical instrument served to : (i) select the facet lens (Fig. 2a), (ii) select two out of the seven receptors visible *in vivo* in the back focal plane of the facet lenslet, and (iii) stimulate these two photoreceptors (R1 and R6) *successively* with $1\mu\text{m}$ -light spots. Sequential stimulation produced an "apparent motion" that would *simulate* a real motion within the small visual field of the selected ommatidium. The H1-neuron responded with a vigorous spike discharge only when the motion was mimicked in the preferred direction (see Fig.2c, top trace). The null response observed for the reverse sequence (Fig.2c, bottom trace) attests to the remarkable sequence-discriminating ability of an EMD, which is indeed *directionally selective* (Franceschini, 1992).

From many experiments of this kind, in which various sequences of light steps and/or pulses were applied to selected receptor pairs, an EMD *block diagram* was obtained and the dynamics and nonlinearity of each block were characterized (Franceschini, 1985, 1992 ; Franceschini et al., 1989). While not unveiling the EMD cellular details - still elusive in both vertebrates and invertebrates - our analysis at least allowed the EMD principle to be understood *functionally*, paving the way for some transcription into another, man-made technology, such as electronics.

Neuromimetic optic flow sensors

In the mid 1980's, we designed a neuromorphic optic flow sensor (Blanes, 1986, Franceschini et al., 1986), the signal processing scheme of which was inspired by what we had learned from the fly EMD. The OF is an angular speed ω [$\text{rad}\cdot\text{s}^{-1}$] that corresponds to the inverse of the time Δt taken by a contrasting feature to travel between the visual axes of two adjacent photoreceptors, separated by an angle $\Delta\varphi$. Our OF sensor processes this delay Δt so as to generate a response that grows monotonically with the inverse of Δt , and hence with the optic flow ω (Fig. 3a). Short delays Δt give higher voltage outputs and vice versa.

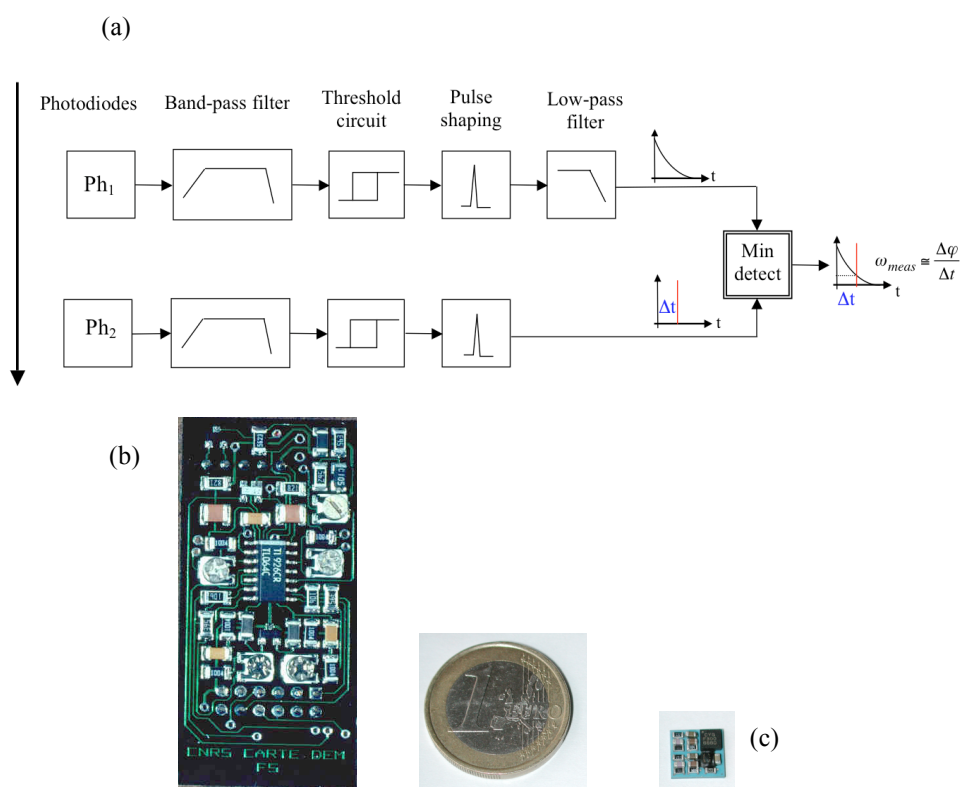


Figure 3: (a) Principle of the electro-optic flow sensor derived from our electrophysiological analyses of the housefly's EMD (Blanes, 1986, Franceschini et al., 1986). (b) purely analogue version (weight 5 grams) built in 1989 for Robot-Fly, whose compound eye housed a ring of 114 EMDs of this type (Pichon et al., 1989 ; Franceschini et al., 1992) (c) hybrid (analogue + digital) version (size : 7mm x 7 mm, mass 0.2 grams) based on a microcontroller and built using Low Temperature Co-fired Ceramics technology (LTCC) (Pudas et al., 2007).

Our scheme is not a “correlator scheme“ (cf Hassenstein and Reichardt, 1956, Reichardt, 1969) and corresponds to the class of “feature-matching schemes“ (Ullman, 1981), where a given feature (here a change in intensity that may represent an edge) is extracted and tracked in time. The photodiode signal of each channel is first *bandpass filtered* (Fig.3a) - resembling the analog signal measured in the large monopolar neurons of the fly lamina (Zettler and Weiler, 1974; Laughlin, 1984). The next step consists of hysteresis thresholding and generation of a unit pulse. In the EMD version built in 1989 for robot Fly (Fig.3b), the unit pulse from one channel was sampling a long-lived decaying exponential function generated by the other channel (Blanes, 1986, Franceschini et al., 1986), via a nonlinear circuit called a minimum detector, to give an output ω_{measured} that grows as a monotonic function of the angular velocity $\omega = \Delta\varphi/\Delta t$ (Fig. 3). The thresholding operation makes the voltage output virtually independent of texture and contrast – unlike the Reichardt correlator – and the circuit responds as well to natural scenes (Portelli et al., 2008). A very similar EMD principle has been conceived, independently, a decade later by C. Koch's group at CALTECH, where it became known as the “facilitate and sample” velocity sensor (Kramer et al., 1995). Yet another variant of our original “time of travel” principle was proposed another decade later (Möckel and Liu, 2006).

Since the original analog design, we have built various versions of OF sensors based on this very principle. In the EMD currently used onboard our aerial robotic demonstrators, the signals are processed using a mixed (analog + digital) approach (Ruffier et al., 2003). Such OF sensors can be small and lightweight (the smallest one weighs only 0.2 grams: Fig.3c) and several of them were also recently integrated on a miniature FPGA (Aubépart et al. 2004, 2008; Aubépart and Franceschini, 2007).

The problem of ground avoidance

To control an aircraft, it has been deemed essential to measure state variables such as groundheight, groundspeed, descent speed, etc. The sensors developed for this purpose - usually emissive sensors such as radio-altimeters, laser rangefinders, Doppler radars, GPS receivers, forward-looking infrared sensors, etc. are far too cumbersome for insects or even birds to carry and to power. The OF sensors evolved by natural flyers over the last few hundred million years are at odds with these avionic sensors. They are based on vision, which is a nonemissive sensory system, and more precisely on OF sensors.

The ventral OF experienced in the vertical plane by flying creatures - including aircraft pilots - is the apparent *angular velocity* ω generated by a point directly below on the flight track (Gibson et al., 1955; Whiteside and Samuel, 1970). As shown in figure 4a, the ventral OF depends on both the groundspeed V_x and the groundheight h and is equal to the ratio between these two variables:

$$\omega = V_x/h \text{ [rad.s}^{-1}\text{]} \quad (\text{Eq.1})$$

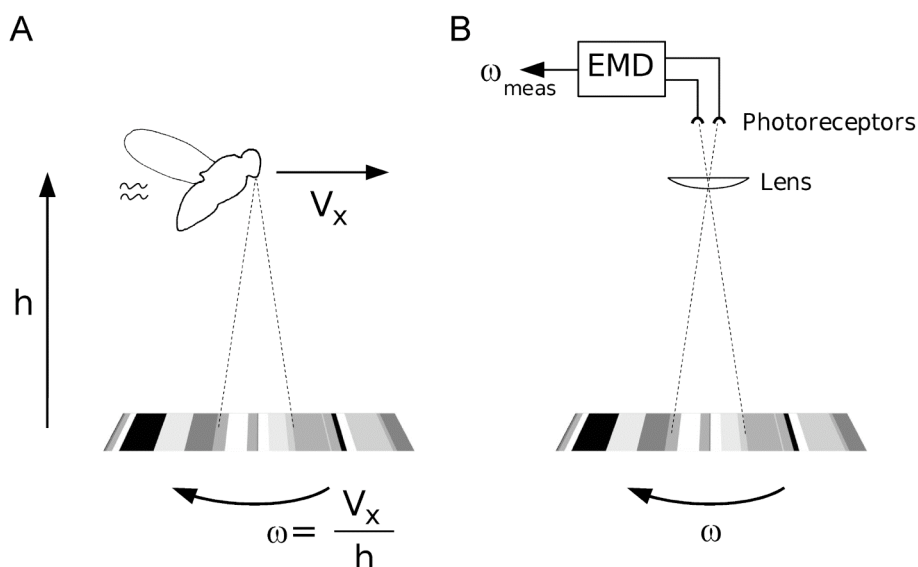


Figure 4: Definition (a) and measurement of the ventral optic flow ω experienced by an insect (or a robot) flying in translation in the vertical plane. (b) an EMD of the type shown in Fig.3, like the EMDs driving the honeybees' VT neurons (Ibbotson, 2001), is able to measure the ventral OF, i.e., the angular speed ω at which any contrasting feature moves under the flying agent (Franceschini et al., 2007).

We know that flies and bees are able to react to the *translational OF* independently of the spatial texture and contrast (David, 1982; Kirchner and Srinivasan, 1989, Srinivasan et al., 1991, 1993; Baird et al., 2005). We also know that some of their visual neurons may be involved in this reaction because they respond monotonically to ω with little dependence on texture and contrast (Ibbotson, 2001; Shoemaker et al., 2005; Straw et al., 2008). Neurons facing downwards can therefore act as ventral *OF sensors*, and thus assess the V_x/h ratio (Fig.4).

Based on laboratory experiments on mosquitoes and field experiments on locusts, Kennedy put forward an “optomotor theory” of insect flight, according to which flying insects maintain a “preferred retinal velocity” with respect to the ground below (Kennedy, 1939, 1951). In response to wind, for example, insects may adjust their groundspeed or groundheight to restore the apparent velocity of the ground features. Kennedy’s hypothesis has been repeatedly confirmed during the last 30 years: both flies and bees were found to maintain a constant OF with respect to the ground while cruising or landing (David, 1978; Preiss, 1992; Srinivasan et al., 1996, 2000, Baird et al., 2006).

The problem is *how* insects may achieve this feat, since maintaining a given OF is a kind of chicken-and-egg problem, as illustrated by equation 1: an insect may hold its ventral OF, ω constant by adjusting either its groundspeed (if it knows its groundheight) or its groundheight (if it knows its groundspeed). Besides, the insect could maintain an OF of 1rad/s (i.e., 57°/s), for instance, by flying at a speed of 1m/s at a height of 1 meter or by flying at a speed of 2m/s at a height of 2m: there is an infinitely large number of possible combinations of groundspeed and groundheight that will give rise to the same “preferred OF”.

Drawing on the experience we had with OF-based visual navigation of a terrestrial robot (Pichon et al., 1989; Franceschini et al., 1992), we attempted early to develop an explicit flight control scheme for aerial navigation in the vertical plane. Our first tentative step on these lines was not particularly successful, because we were cornered in the general notion that prevailed in those days that insect navigation relies on *gauging range* (Kirchner and

Srinivasan, 1989; Srinivasan et al., 1991; Franceschini et al., 1992; Srinivasan, 1993). In the experimental simulations we performed in 1994, for example (Mura and Franceschini, 1994), we assumed that the insect (or the robot) would know its groundspeed V_x (by whatever means), so that by measuring ω it would be able to gauge the distance h from the ground (Eq.1) and react accordingly to avoid it. Although this procedure is still used in robotics (see, e.g., Barber et al, 2005; Srinivasan, 2006; Garratt and Chahl, 2008), where groundspeed can be determined (e.g., via GPS), this makes the way insects operate all the more elusive. In 1999, we established (in simulation) *how* a rotorcraft (or an insect) might be able follow a terrain (Fig. 5a) and land (Fig. 5b) on the sole basis of OF cues, *without measuring its groundspeed and groundheight* (Netter and Franceschini, 1999).

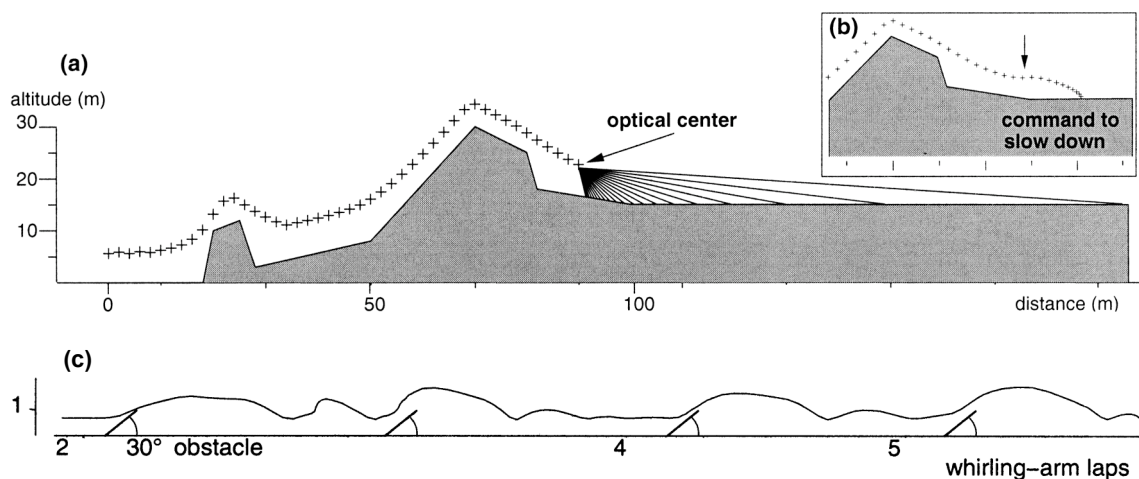


Figure 5: Optic flow based terrain following and landing of a miniature helicopter whose eye (20 pixels, 19 EMDs) covers a frontal FOV of 75° in the vertical plane, centered at 40° below the horizon (a) Simulation of nap-of-the-earth flight (initial conditions: height: 5m, speed $2\text{m}\cdot\text{s}^{-1}$; iteration step 1s). (b) Landing initiated by simply decreasing the rotorcraft horizontal speed at every iteration while retaining the same request to maintain a reference OF value (Netter and Franceschini, 1999). (c) actual flight path of the tethered FANIA rotorcraft, which repeatedly jumped over a 30° rising terrain (Netter and Franceschini, 2002).

The landing manoeuvre was achieved under permanent visual feedback from a 20-pixel forward looking eye (with 19 EMDs). The driving force causing the progressive loss in altitude was the decrease in the horizontal flight speed, which occurred when the rotorcraft (or the insect) decreased its speed to land - either voluntarily or in the presence of a headwind. The landing trajectory obtained in this simulation (Fig.5b) already resembles the final approach of bees landing on a smooth surface (Srinivasan et al, 1996). The principle was first validated onboard FANIA, a miniature tethered helicopter having a single (variable pitch) rotor, an accelerometer and a forward looking eye with 20 pixels (and, therefore, 19 EMDs) arranged in the frontal meridian (Netter and Franceschini, 2002). This 0.8-kg rotorcraft had three degrees of freedom (surge, heave and pitch). Mounted at the tip of a flight mill, the robot lifted itself by increasing its rotor collective pitch. Upon remotely inclining the servo-vane located in the propeller wake, the operator made the helicopter pitch forward by a few degrees so that it gained speed and, therefore, climbed to maintain a reference OF with respect to the terrain below. FANIA was able to jump over a rising terrain by increasing its collective pitch as a function of the fused signals from its 19 EMDs (Fig.5c).

The optic flow regulation principle

In spite of this early success to explain how an insect could navigate on an OF basis, we considered that Kennedy’s insightful “optomotor theory” was calling for a clear formalization that would bring to light:

- the flight variables really involved
- the sensors really required
- the dynamics of the various system components
- the causal and dynamic links existing between the sensory output(s) and the variable(s) to be controlled
- the point of application of the various disturbances that an insect will experience in flight and the variables it will have to control to compensate for these disturbances.

We came up with an autopilot called OCTAVE (OCTAVE stands for Optical altitude Control sysTEM for Autonomous VEHICLES) that is little demanding in terms of neural (or electronic) implementation and could be just as appropriate for insects as it would be for aircraft (Ruffier & Franceschini, 2003). A ventral OF sensor was integrated into a feedback loop that would drive the robot’s lift, and thus the groundheight, so as to compensate for any deviations of the OF sensor’s output from a given set point (Ruffier and Franceschini, 2003, 2004a,b, 2005; Franceschini et al., 2007). As we will see, this simple autopilot (Fig.6a) enabled a micro-helicopter to perform challenging tasks such as take-off, terrain following, reacting suitably to wind, and landing.

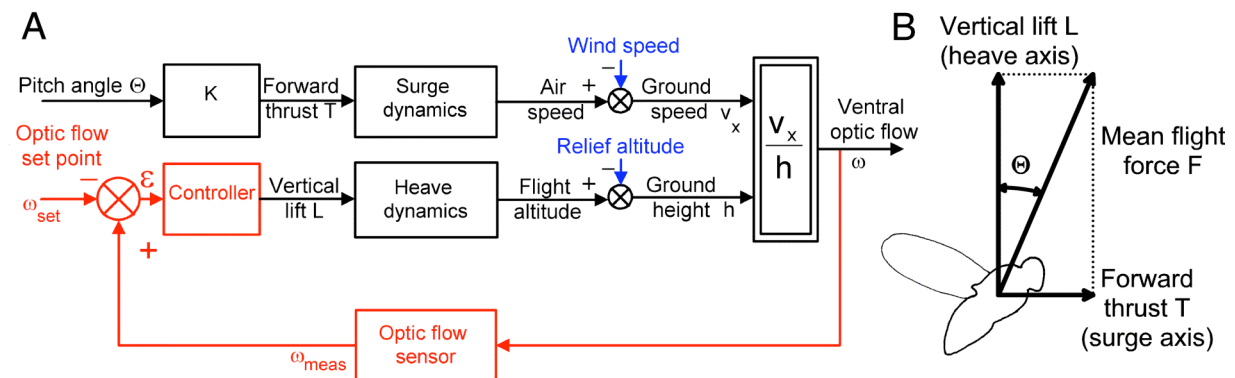


Figure 6: (A) The OCTAVE *optic flow regulator* (bottom feedback loop) controls the mean flight force vector and hence the lift, and hence the groundheight, so as to maintain the ventral optic flow ω constant and equal to the set-point ω_{set} . (B) Flies, like helicopters, pitch forward slightly to increase their forward thrust, and hence their airspeed. As long as they pitch forward by $\theta < 10^\circ$, the lift component L does not incur any major loss (Franceschini et al., 2007).

The OCTAVE autopilot can be said to be an *OF regulator*. The word ‘regulator’ is used here as in control theory to denote a *feedback control system* designed to maintain an output signal constantly equal to a given set point. The Watt flyball governor from the 18th century, for instance, was not only one of the first servomechanisms ever built: it was also the very first *angular speed regulator*. It served to maintain the rotational speed of a steam engine shaft at a given set point, whatever interferences occurred as the result of unpredictable load disturbances. The Watt regulator was based on a rotational speed sensor (meshed to the output

shaft), whereas the *OF regulator* is based on a noncontact rotational speed sensor - an *OF sensor* - that measures the ventral OF (again in rad/s).

Specifically, the OF signal ω_{meas} delivered by the OF sensor (see Fig.6a) is compared with the OF set point, ω_{set} . The comparator produces an error signal: $\epsilon = \omega_{meas} - \omega_{set}$ which drives a controller adjusting the lift L , and thus the groundheight h , so as to minimize ϵ . All the operator does is to set the pitch angle Θ and therefore the airspeed (see figure 6A): the *OF regulator* does the rest, that is, it attempts to keep ω constant by adjusting the groundheight h proportionally to the current groundspeed V_x . In the steady state ($t = \infty$), $\omega_{meas} \approx \omega_{set}$, and the groundheight becomes proportional to the groundspeed .

$$h = K V_x \quad (\text{with } K = l/\omega_{SET} = \text{constant}) \quad (\text{Eq. 2})$$

The controller includes proportional and derivative (PD) functions, which ensure closed-loop stability in the groundspeed range of $0\text{-}3\text{m.s}^{-1}$. Controlling F (via the rotor speed) actually affects not only L but also T . This *coupling* is negligible, however, because Θ is always $\leq 10^\circ$ for the highest speed attained (3m.s^{-1}), so that the ensuing change in L is at least 6-times ($\cotan 10^\circ$) greater than the change in T .

A micro-helicopter equipped with an OF sensor and an OF regulator

We tested the idea that insects may be equipped with a similar *OF regulator* by comparing the behavior of insects with that of a “seeing helicopter” placed in similar situations. The robot we built (Fig.7a) is a micro-helicopter (MH) equipped with a simple, 2-pixel ventral eye driving an EMD acting as an OF sensor (Fig.7a). The 100-gram robot is tethered to an instrumented flight mill consisting of a light pantographic arm driven in terms of its elevation and azimuth by the MH’s lift and forward thrust, respectively (Fig.7b).

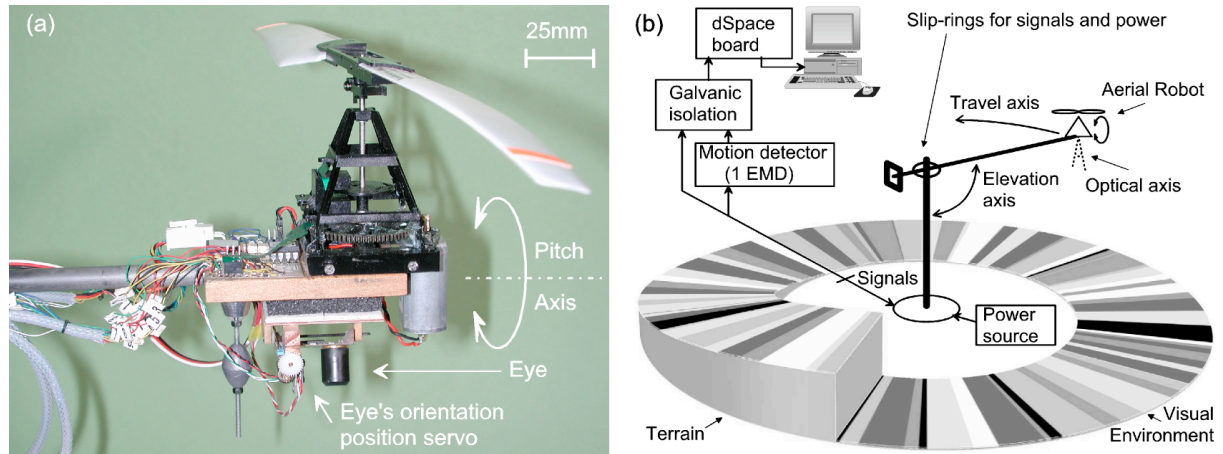


Figure 7: (a) 100-gram Micro-helicopter (MH) equipped with a ventral *OF sensor* (Fig.3e) and the *OF regulator* shown in A. (b) The MH can be remotely pitched forward by a small angle Θ while keeping its roll attitude. It lifts itself and circles counterclockwise at speeds up to 3m/s and heights up to 3m over a large arena (outside diameter: 4.5m), giving rise to the flight patterns given in Figs. 8-9 The flight mill is equipped with ground-truth azimuthal and elevation sensors with which the position and speed of the MH can be monitored accurately in real time (Ruffier and Franceschini, 2003).

Any increase in the rotor speed causes the MH to rise, and the slightest (operator mediated) forward (“nose-down”) tilting by a few degrees produces a forward thrust component that causes the MH to gain forward speed. The flight mill is equipped with ground-truth azimuthal and elevation sensors that allow the position and speed of the MH to be monitored at high accuracy and in real time. Since the MH purpose was to demonstrate a basic principle, it was equipped with an elementary ventral eye composed of only two photoreceptors driving a single Elementary Motion Detector (EMD) built according to the principle shown in Fig.3a (Ruffier and Franceschini, 2003, Ruffier et al., 2003).

Micro-helicopter’s versus insects’ behavioral patterns

OCTAVE’s *OF regulator* scheme results in the behavioral patterns shown in Fig.8. Between arrowheads 1 and 2, the operator simply pitched the MH forward rampwise by an angle $\Delta\Theta = +10^\circ$. The ensuing increase in groundspeed V_x (up to $3\text{m}\cdot\text{s}^{-1}$, see Fig.8B) automatically made the MH take off, since the feedback loop consistently increased h proportionally to V_x to comply with equation (3).

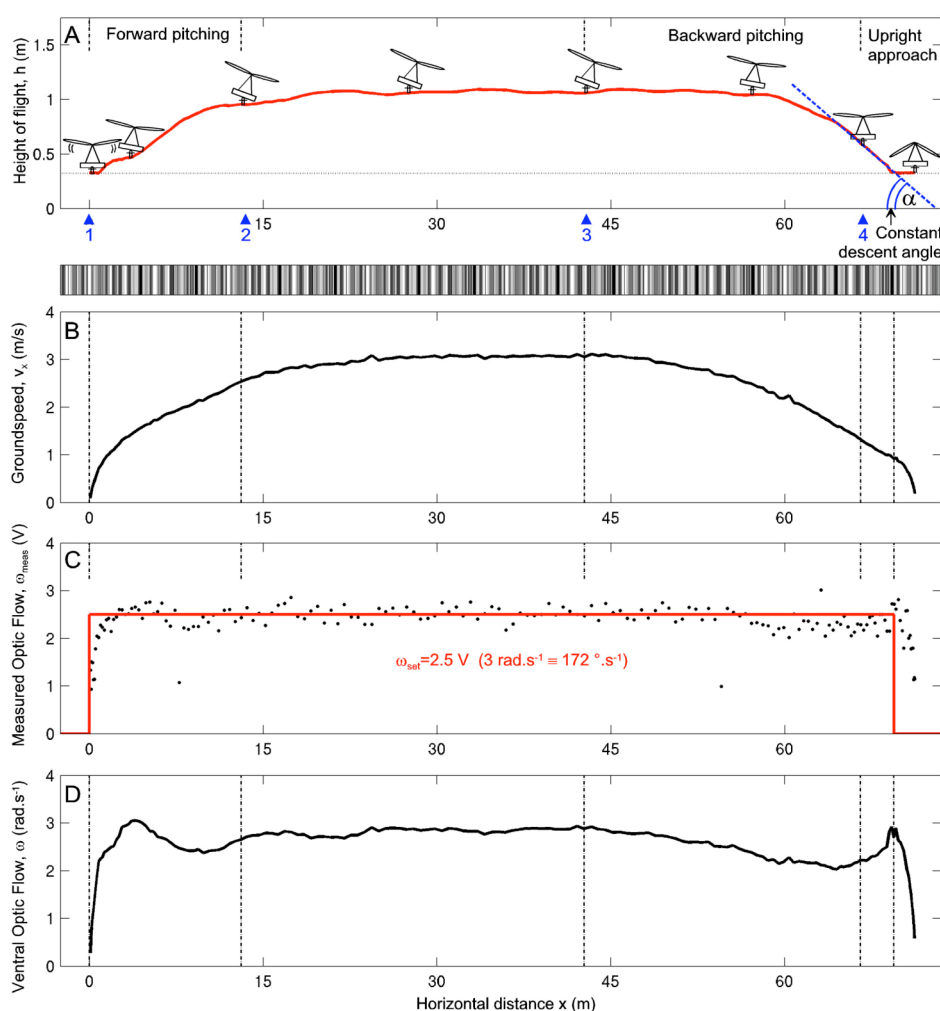


Figure 8: Flight variables monitored during a 70-meter flight of the micro-helicopter over a flat, randomly textured pattern (shown at the bottom of (A)), including take-off, level flight and landing at a constant descent angle. (a) Flight path consisting of about six laps on the circular test arena. (B) Groundspeed V_x . (C) Output ω_{meas} of the OF sensor. (D) Actual OF, ω (calculated as V_x/h) resulting from the behavioral reaction (Franceschini et al., 2007).

Once reaching a constant speed, the MH flew level at a groundheight of approximately 1m - the value imposed by the OF set point $\omega_{set} = 3\text{rad}\cdot\text{s}^{-1} = 172^\circ\cdot\text{s}^{-1}$ (Fig.8C). After covering 42m, the MH was pitched backwards rampwise by an opposite angle $\Delta\Theta = -10^\circ$ (between arrowheads 3 and 4), and the ensuing deceleration (see Fig.8B) effectively produced an automatic descent and landing – a safe landing maneuver since it is performed “under visual control”. The actual OF (Fig.8D) is seen to have been held relatively - but not perfectly - constant throughout the journey, even during the takeoff and landing maneuvers where the groundspeed can be seen to vary considerably (Fig.8B).

Figure 9 shows that the various robot’s flight patterns are extremely robust and reproducible, including those over a rising terrain and in the presence of wind.

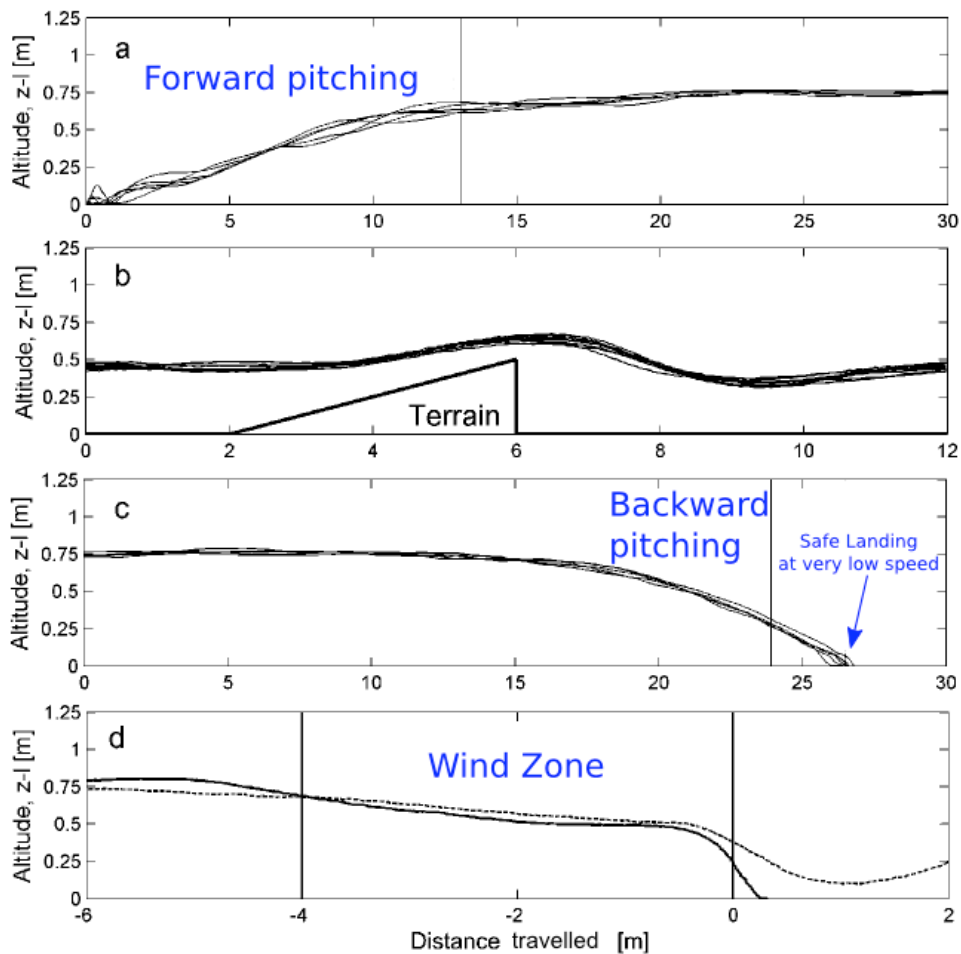


Figure 9: Performance and reproducibility of the micro-helicopter’s flight path in the longitudinal plane. (a) automatic take-off obtained by gradually pitching the rotorcraft forward (nose-down) by 10° from the vertical. (b) automatic terrain following over the rising terrain shown in Fig.6d. (c) automatic approach and landing upon gradually raising the rotor axis vertically (nose-up). (d) a light headwind made the rotorcraft descend (dotted trajectory). A strong headwind forced the MH to land (continuous curve) at negligible vertical and forward speeds (Ruffier and Franceschini, © 2004 IEEE)

The *OF regulator* concept was found to account for a series of puzzling, seemingly unconnected flying abilities observed in various insect species, as summarized below: (details in Franceschini et al., 2007):

- *automatic terrain following*. A gradual increase in relief constitutes a “disturbance” that impinges on the system at a particular point (see Fig.7a). The closed feedback loop overcomes this disturbance by increasing the flight altitude, resulting in a constant groundheight over the rising terrain (Fig.9b). This may account for the well-documented terrain and canopy following abilities of migrating insects (e.g., Srygley and Oliveira, 2001).
- *suitable reactions to headwind*. Windspeed is a disturbance that impinges on the system at a different point (see Fig.6a) and reduces the groundspeed. The feedback loop overcomes this disturbance by forcing the robot to descend (and even to land smoothly by strong wind) (Fig.9d). A similar reaction was observed in locusts, honeybees and dung beetles.
- *flying over a no-contrast zone*. Here the OF sensor fails to respond, which irremediably causes the robot to crash, just as honeybees crash into mirror-smooth water (Heran and Lindauer, 1963).
- *landing on a flat surface*. During the *final approach*, which starts when the MH has regained its completely upright position (arrowhead 4 in Fig.8a and vertical line in Fig.9c), the *OF regulator* forces the MH to land smoothly at a *constant descent angle*, α , which can be calculated as follows:

$$\alpha = -\arctan\left(\frac{1}{\omega_{set}\tau}\right) \quad (Eq. 3)$$

where ω_{set} [rad.s⁻¹] is the OF set-point, and τ [s] is the MH’s *surge time constant* ($\tau_{MH} = 2.15s$).

Interestingly, honeybees were also observed to land with a constant slope on flat surfaces, but the way they may achieve this feat has been explained quite differently. According to Srinivasan et al. (2000), landing bees would follow two rules: "(a) adjusting the speed of forward flight to hold constant the angular velocity of the image of the surface as seen by the eye, and (b) making the speed of descent proportional to the forward speed". By contrast, the *OF regulator* automatically generates smooth landing with a constant slope while adjusting neither the forward speed nor the speed of descent.

The OF set point ω_{set} is the reference signal that the feedback loop must maintain constant under all circumstances. ω_{set} would thus correspond to Kennedy’s early ideas about a “preferred angular velocity of image movement” (Kennedy, 1939, 1951). By increasing its ω_{set} (see Fig.7A), the flier will follow the terrain at a lower height, as typically observed in the case of the MH (see Ruffier and Franceschini, 2003, Fig.9a). Conversely, by setting ω_{set} near zero, the animal will rise farther from the ground, as also typically observed on the MH. This OF set point ω_{set} may well be under the control of other (e.g., visual or olfactory) sensors, but it may also depend on other external and/or internal factors such a ‘drive for migration’ (in the case of locusts: Preiss, 1992)

Taken together, these data show that an aerial vehicle equipped with an *OF regulator* will be able to take off, navigate over flat or rising terrain, react sensibly to headwind and land without ever measuring and holding any groundheights, groundspeeds or descent speeds. A similar principle was recently applied to a 0.4kg flying wing, which by flying at a constant cruise speed (imposed by an extra airspeed regulator) was able to maintain its altitude from its ventral OF measurement (Beyeler et al., 2009).

Micro-hovercraft's versus honeybees' behavioural patterns

Behavioral experiments on several insect species have long shown that motion perceived by the *lateral* part of their compound eyes affects the forward thrust, and hence the forward speed (rev.: Franceschini et al., 2007). Firstly, when flying through a *tapered corridor*, honeybees slowed down as they approached the narrowest section and speeded up when the corridor widened beyond this point (Srinivasan et al., 1996). The authors concluded that bees tended to adjust their speed proportionally to the local corridor width by regulating the image velocity. Secondly, when flying through a *straight corridor*, honeybees tended to fly along the midline (Srinivasan et al., 1991). To explain this “centering behavior”, the authors hypothesized that bees were balancing the speeds of the retinal images (i.e., the lateral OFs) of the two walls, an hypothesis that subsequently gave rise to many wheeled and aerial robots capable of centering in a corridor (e.g., Coombs and Roberts 1993; Duchon and Warren, 1995; Santos-Victor et al., 1995).

We recently found, however, that honeybees trained to fly along a *larger* corridor do not systematically center on the corridor midline (Fig.10b,c). They keep remarkably *close to one wall*, even when part of the opposite wall is missing (Fig.10d). Distance from that wall (D_R or D_L) and forward speed V_x were on average such that the speed-to-distance ratio (i.e., the lateral OF) was maintained practically constant, at about $230^\circ/s$ in our 95-cm wide corridor (Serres et al., 2008a).

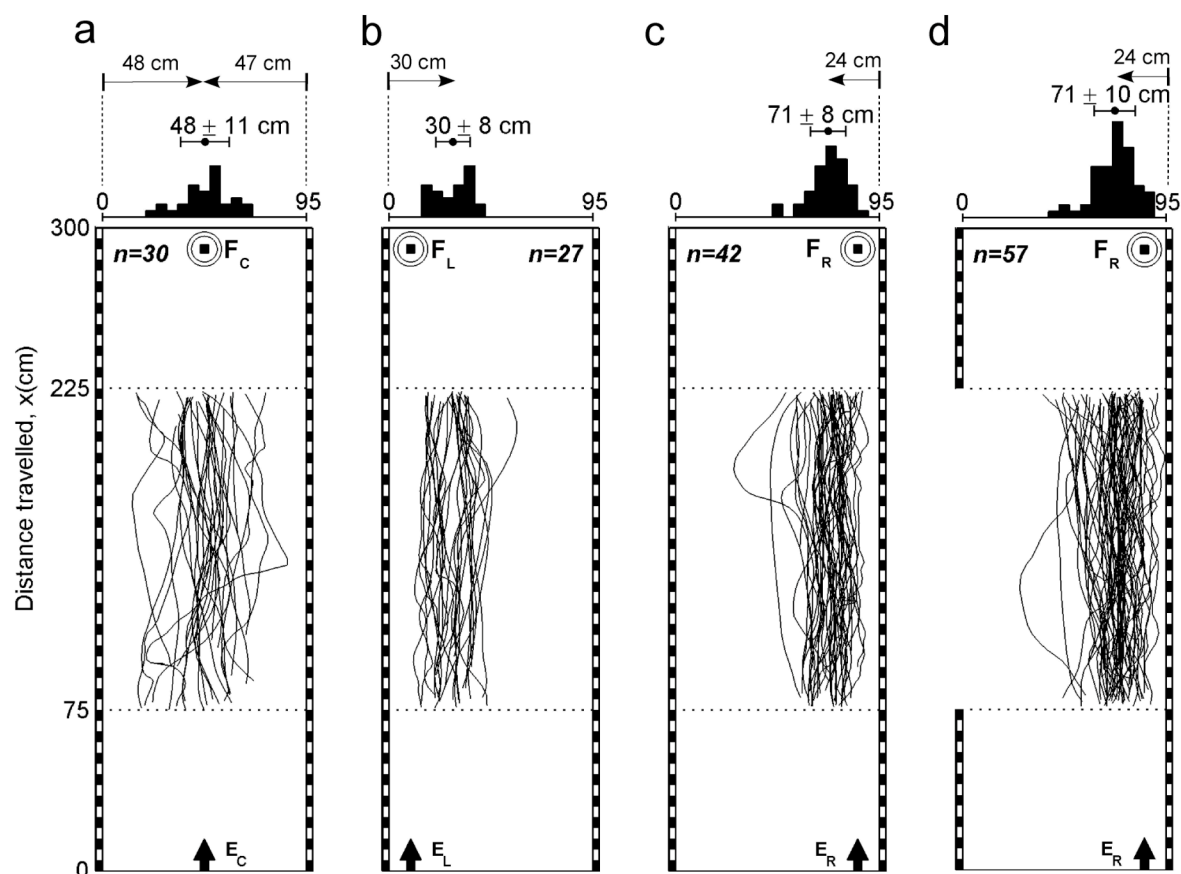


Figure 10: Honeybees' *centering* and *wall-following* behaviors. Bees were trained to enter a wide (width 0.95m) 3-meter long corridor, formed by two 0.25-m high walls lined with vertical white-and-grey stripes (period 0.1m; contrast $m = 0.41$). The bee's entrance (E_C) and the feeder (F_C) were placed either on the corridor midline (a) or on one side (b, c, d). In (d), part of the left wall was removed during the trials. Mean distances distribution as shown on top (Serres et al., 2008a).

With a view to explaining the various honeybees' behaviors observed in the various corridors, we came up with the design of the LORA III autopilot (LORA III stands for Lateral Optic flow Regulator Autopilot, mark III), which is able to control both the forward speed V_x of an aerial vehicle and its lateral distances D_R and D_L from the two corridor walls jointly, *without ever measuring speed and distances* (Fig.11A) (Serres et al., 2008b). A micro-hovercraft (HO) was used, which can produce insect-like forward and sideward slips independently, because the two added lateral thrusters $LT1$ and $LT2$ (Fig.11B,C) make it *fully actuated*. It travels at a constant altitude ($\sim 2\text{mm}$) and senses the environment with two laterally oriented eyes measuring the right and left OFs. The HO's heading is maintained along the X-axis of the corridor (Fig.11C) by a heading lock system which compensates for any yaw disturbances by controlling the two rear thrusters *differentially*. This system mimics the honeybee's heading lock system, which is based on a polarized light compass (Rossel and Wehner, 1972) and gives the insect an impressively straight course even in the presence of wind (Riley and Osborne, 2001).

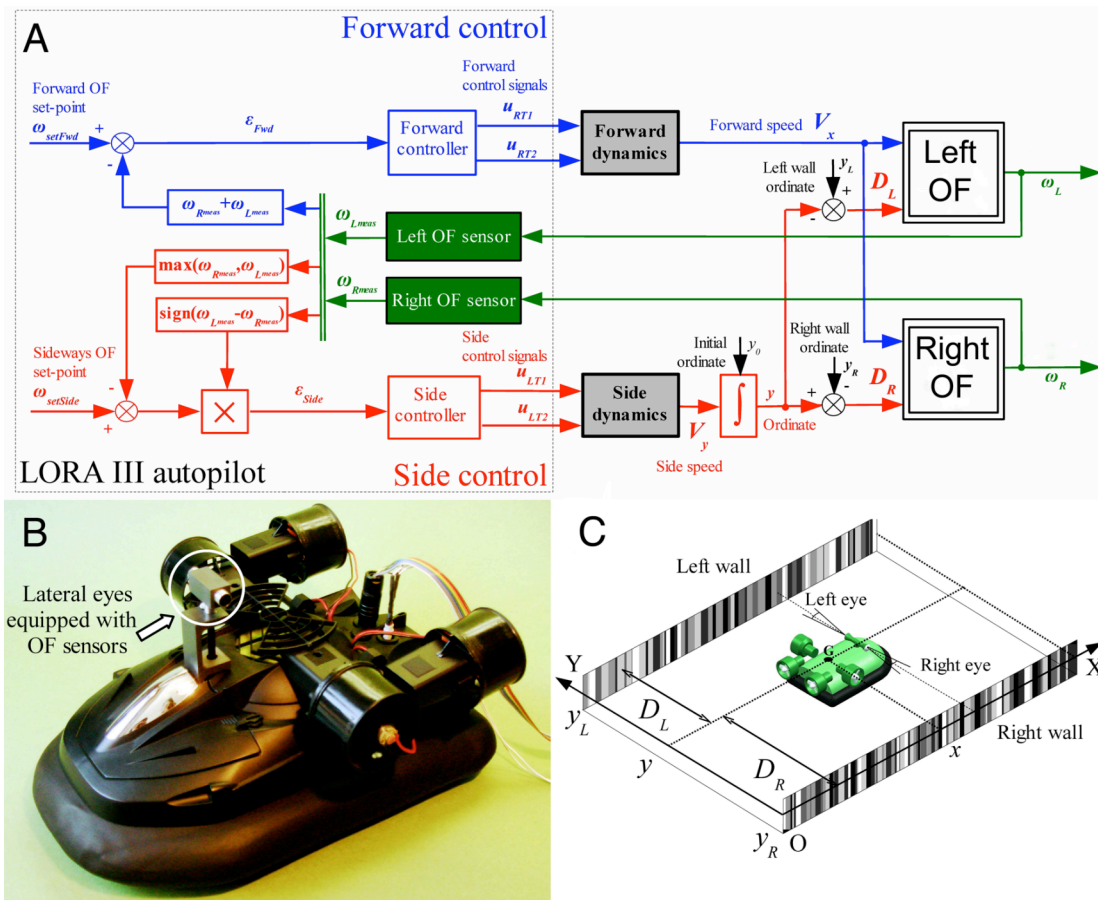


Figure 11: (A) LORA III autopilot enabling a hovercraft to navigate in a corridor by controlling its forward speed and its distance to the walls *jointly*, *without measuring any speeds or distances*. (B, C) *fully actuated* hovercraft (HO) equipped with two OF sensors looking sidewards at an angle of $+90^\circ/-90^\circ$. The corridor walls are randomly textured (Serres et al., 2008b).

LORA III autopilot is based on only two OF sensors (one looking to the right, one to the left). The forward speed V_x is controlled (via a proportional-integral controller) by the error signal ϵ_{Fwd} between the *sum* of the two OFs (right and left) and the forward OF set-point ω_{setFwd} .

The side slip speed V_y , and thus the lateral distances D_L and D_R to the walls, is controlled (via a proportional derivative controller) by the error signal ϵ_{Side} between the *larger* of the two OFs and the sideways OF set-point $\omega_{setSide}$. The HO's behavior is entirely determined by these two OF set points: $\omega_{setFwd} = 300^\circ/s$ and $\omega_{setSide} = 230^\circ/s$.

Simulation experiments where the HO navigated in a straight or tapered corridor accounted for all the honeybees' behaviors reported above (Serres et al., 2008b). Fig.12 illustrates, for example, the HO's behavior in a tapered corridor. Whatever the position of its initial ordinate y_0 , the HO automatically decelerated on approaching the narrowest section of the corridor and accelerated when the corridor widened. It can be seen that the *forward control system* succeeded in keeping the *sum* of the two lateral OFs measured nearly constant and equal to the forward OF set-point $\omega_{setFwd} = 300^\circ/s$ (Fig.12c). Likewise, the *side control system* succeeded in keeping the *larger* of the two lateral OFs measured practically constant and equal to the sideways OF set-point $\omega_{setSide} = 230^\circ/s$ (Fig.12e). The result is that the HO automatically tuned both its groundspeed and its distance to the walls jointly, without any knowledge about the current corridor width, the groundspeed and the clearance from the walls.

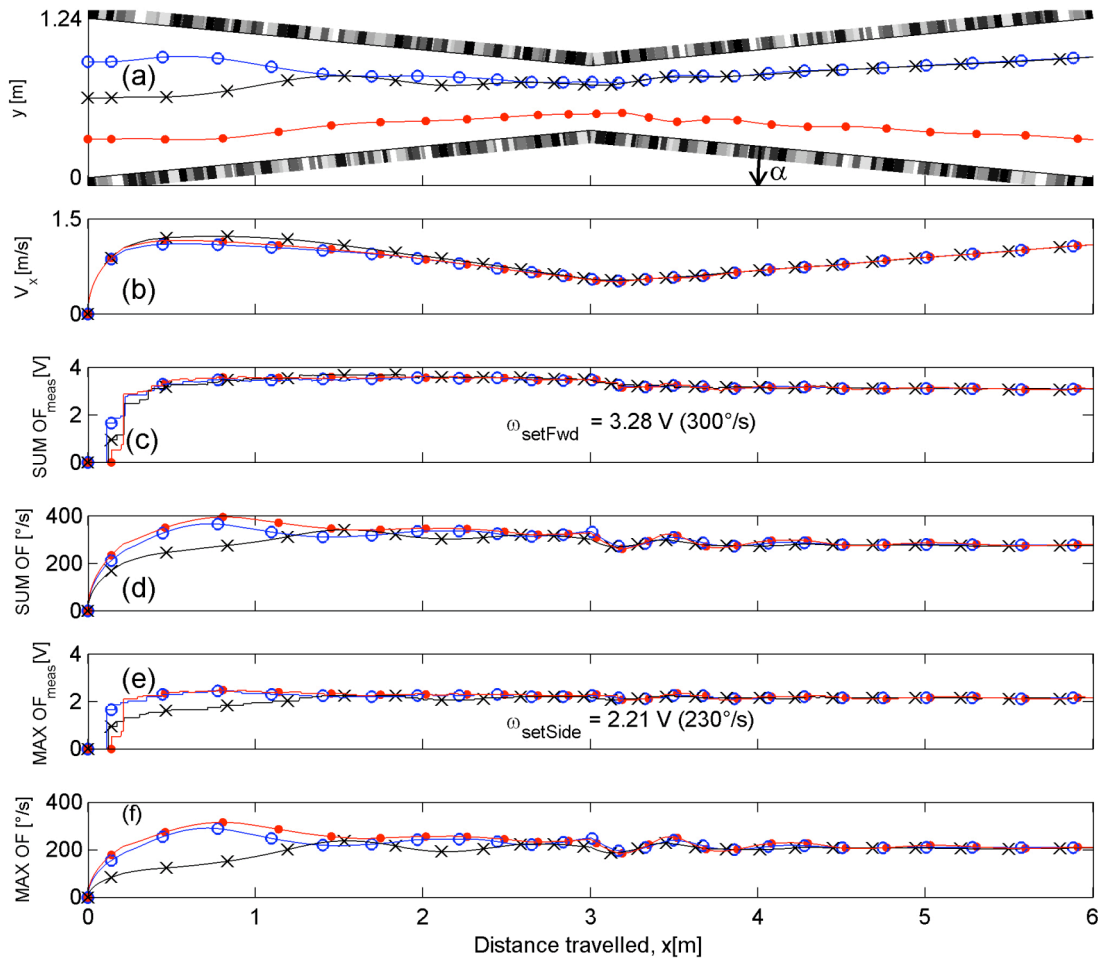


Figure 12: Simulated navigation of the hovercraft (HO) along a tapered corridor, requiring no data on the corridor width, tapering angle α , nor any measurements of groundspeed and distance to the walls. (a) Simulated trajectories of the HO moving to the right along the corridor (tapering angle $\alpha = 7^\circ$) with three initial ordinates y_0 (open dots: $y_0=0.90m$, crosses: $y_0=0.60m$, full dots: $y_0 = 0.30m$). (b) Forward speed profile. (c,d) sum and maximum of the two lateral OFs *measured*, respectively. (e,f) sum and maximum of the two *actual* OFs, respectively (Serres et al. 2008b).

The field of view (FOV) of the eyes and the provocatively small numbers of pixels (four) and EMDs (two) will obviously need to be increased for dealing with navigation in more sparsely textured environments. It will also be necessary to control the heading direction (e.g., Zufferey, 2008) to enable the HO to successfully negotiate more challenging corridors including L-junctions and T-junctions (cf Humbert and Hyslop, 2010)

Conclusion

In studying the types of operations that insects may perform to guide their flight on the basis of optic flow (OF) cues, we came up with several bio-inspired autopilot principles that harness the power of the *translatory OF* parsimoniously and therefore offer interesting prospects for MAV autonomous guidance. The micro-helicopter's outstanding visuo-motor performance (Fig.7,8) suggests *how* insects and MAVs may take off, follow terrain and land if they are equipped with OF sensors facing the ground and an *OF regulator* that servoed the measured OF to a given set point (Fig.6). The great advantage of this autopilot is that it requires neither *measuring* nor *computing* nor *regulating* (i.e., holding constant) any groundspeeds or groundheights. The only variable it needs to *measure* and *regulate* is the OF - a variable that can be accessed straight forward by dedicated sensors called OF sensors (Fig.3). The recent finding that bees gradually descend when they fly in a corridor the floor of which is moved in the same direction as their flight, is fully consistent with the OCTAVE autopilot model (Portelli et al., 2010a). The OCTAVE principle differs markedly from another OF-based navigation strategy which requires measuring not only the ventral OF but also the groundspeed (e.g., from GPS), with an aim to estimate the groundheight (see equation (2)) (Barber et al, 2005; Srinivasan et al., 2006, Garratt and Chahl, 2008).

OCTAVE and LORA III autopilots consist of *interdependent OF regulators*, which control the lift, lateral thrust, and forward thrust, on which the groundheight, lateral position and groundspeed, respectively, depend. The block diagrams (Fig.6 and Fig.10) show which variables need to be *measured*, which ones are *controlled* and which ones are *regulated*, as well as the point of application of the various disturbances.

In contrast with the control schemes presented by Conroy et al. (2009) for a quadrotor navigating a straight corridor, OCTAVE's task is not to hold a "desired height" and LORA III's task is not to hold a "desired forward speed" and a "desired lateral position" in the corridor. Before entering the corridor, our hovercraft does not know how fast it will eventually fly and whether or not it will center or follow one wall: it is the environment itself that constrains both its speed and its distance to the walls, depending on the OF set points (Fig.12). These explicit control schemes account for a series of flying abilities observed in numerous insect species, including honeybees' habit of landing at a constant slope and their flight pattern along a straight or tapered corridor. Our recent finding that bees do not center systematically in a corridor but may follow a wall unilaterally (Fig.9d) cannot be accounted for by the "optic flow balance hypothesis" (Srinivasan et al., 1991) but is convincingly accounted for by the LORA III model, where "centering behavior" arises as a particular case of "wall-following behavior" (Serres et al., 2008b). OCTAVE and LORA III interdependent *OF regulators* were recently combined in a comprehensive model, called ALIS (Autopilot using an Insect-based vision System), which allows a simulated bee to travel safely along (horizontally or vertically) tapered tunnels, by automatically controlling both its speed and its clearance from the right wall, left wall, ground and roof, without ever estimating any groundspeeds or distances (Portelli et al, 2010). The simulated bee navigates on the basis of two parameters alone: the forward OF set-point and the positioning OF set-point. While it is

conceivable that on board insects the OF set points may depend on either innate, internal or external factors, MAVs could receive their OF set-points from the control station via a radio-link.

Once engineered further, the OF-feedback control systems we have described here could serve to improve navigation aids and automatic maneuvers. When measured on a commercial aircraft, a *ventral* OF greater than the set point would mean that the current altitude is "too low for the current groundspeed" (Franceschini et al., 2003). Installed on board a MAV, the OCTAVE *autopilot* would enable it to automatically take off, fly level at a groundheight proportional to the groundspeed, follow shallow terrains, make it react automatically to unpredictable headwind or tailwind disturbances (by descending or climbing, respectively), and land safely (Franceschini et al., 2003, Ruffier and Franceschini, 2004, 2005b). Both OCTAVE and LORA III could potentially guide MAVs indoors or through complex terrains such as mountain or urban canyons, without using any computationally intensive visuomotor algorithms. Since these autopilots do not rely on GPS and ILS, and do not require any bulky (and power-hungry) emissive sensors such as RADARs, SONARs, FLIRs, or laser rangefinders, they can be of very small size, lightweight and power-lean, and therefore meet the challenge of future insect-scale MAVs. For the same reasons, these simple autopilots could potentially be adapted to micro- or nano-space vehicles (MSVs) landing on command on other celestial bodies or performing rendezvous and docking missions in space. A recent paper presented the first simulation experiment conducted in our laboratory, showing an OCTAVE-based descent to the Moon (Valette et al., 2010). Over the last 2.6 km, the lander actuated its thrusters as a function of its pitch, so as to brake from 1800 km/h down to only 15km/h. This descent (from 500m down to 10m above the Moon surface) occurred "under visual control", thanks to the ventral OF sensor and the OF regulator, without using any altimeters or speedometers. Throughout descent, the lunar lander maintained an approximately constant OF of about $0.3\text{rad}\cdot\text{s}^{-1}$ (i.e., 17.2° s^{-1}).

An aerial Martian rover equipped with more elaborate OCTAVE and LORA III autopilots could take off autonomously and explore an area, skimming the ground and hugging the walls of a canyon, and adapting its groundspeed and clearance from the walls automatically to the width of the canyon. With ground and obstacle avoidance at a premium, the rover could perform its mission successfully in uncharted environments, despite being unaware of its own groundspeed and altitude at all times. The orbiter (or the Earth-based control station) would simply be required to send the rover a set of *low bandwidth* signals: the values of the OF set points (Franceschini, 2009).

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References

- Aubépart F, Franceschini N (2007) Bio-inspired optic flow sensors based on FPGA: application to micro-air vehicles. *Journal Microprocessors and Microsystems* 31, 408-419
- Aubépart F, El Farji M, Franceschini N (2004) FPGA implementation of elementary motion detectors for the visual guidance of micro-air vehicles. *Proceedings of IEEE International Symposium on Industrial Electronics (ISIE'2004)*, Ajaccio, France, pp. 71-76
- Baird E, Srinivasan MV, Zhang SW, Cowling A (2005) Visual control of flight speed in honeybees. *Journal of Experimental Biology* 208: 3895-3905
- Baird E, Srinivasan MV, Zhang SW, Lamont R, Cowling A (2006) Visual control of flight speed and height in the honeybee. In: S. Nolfi et al. (eds.), *From Animals to Animats* 9, 4095, pp. 40-51
- Barber DB, Griffiths SR, McLain TW, Beard RW (2005) Autonomous landing of miniature aerial vehicles. In: *Proceedings of American Institute of Aeronautics and Astronautics Conference*
- Beyeler A, Zufferey JC, Floreano D. Vision-based control of near-obstacle flight. *Autonomous Robots* 27, 2009: 201-219
- Blanès, C (1986) Appareil visuel élémentaire pour la navigation à vue d'un robot mobile autonome. *MS thesis in Neuroscience*, University of Aix-Marseille II, Marseille, France
- Borst A, Haag J (2002) Neural networks in the cockpit of the fly. *Journal of Comparative Physiology A* 188: 419-437
- Braitenberg V (1967) Patterns of projection in the visual system of the fly, I/Retina-Lamina projections. *Experimental Brain Research* 3: 271-298
- Buchner E (1984) Behavioral analysis of spatial vision in insects In: Ali, M. (ed.) *Photoreception and Vision in Invertebrates*, New-York : Plenum, pp. 561-621
- Card G, Dickinson M (2008) Visually Mediated Motor Planning in the Escape Response of *Drosophila*. *Current Biology* 18: 1300-1307
- Conroy J, Grémillon G, Ranganathan B, Humbert JS (2009) Implementation of wide-field integration of optic flow for autonomous quadrotor navigation. *Autonomous Robots* 27 : 189-198
- Coombs D, Roberts K (1993) Centering behavior using peripheral vision. In : Proc. IEEE Conf. on Computer Vision and Pattern Recognition, New York, USA (1993)
- David C (1978) The relationship between body angle and flight speed in free-flying *Drosophila*. *Physiological Entomology* 3: 191-195
- David C (1982) Compensation for height in the control of groundspeed by *Drosophila* in a new 'barber's pole' wind tunnel. *Journal of Comparative Physiology A* 147: 1432-1351
- Duchon, A.P., Warren, W.H. (1994) Robot navigation from a Gibsonian viewpoint. In: *Proc. IEEE Intern. Conf. on Systems, Man and Cybernetics (SMC)*, San Antonio, USA, pp. 2272-2277
- Egelhaaf, M, Borst A (1993) Movement detection in Arthropods. In: F Miles, J Wallman (eds.) *Visual motion an its role in the stabilization of gaze*, Amsterdam: Elsevier, pp. 53-77
- Franceschini N (1975) Sampling of the visual environment by the compound eye of the fly: fundamentals and applications, In: A Snyder, R Menzel (eds) *Photoreceptor Optics*, Berlin : Springer, Chapt. 17, pp. 98-125
- Franceschini N (1984) Chromatic organisation and sexual dimorphism of the fly retinal mosaic. In: A Borsellino, L Cervetto, L. (eds.) *Photoreceptors* pp. 319-350
-

- Franceschini N (1985) Early processing of colour and motion in a mosaic visual system. *Neuroscience Research*, Suppl. 2: 517-549
- Franceschini N (1992) Sequence-discriminating neural network in the eye of the fly. In: FHK. Eeckman (ed.) *Analysis and Modeling of Neural Systems*, Norwell, USA, Kluwer Acad. Pub., pp. 142-150.
- Franceschini N (2007) Sa majesté des mouches. In: JP Gex, E Fox-Keller (eds.) *Voir l'Invisible*, Paris: Omniscience, pp 28-29
- Franceschini N (2009) Towards Automatic Visual Guidance of Aerospace Vehicles : From Insects to Robots. *Acta Futura* 3 : 15-34
- Franceschini N, Blanes C, Oufar L (1986) Passive, noncontact optical velocity sensor *Technical Report ANVAR/DVAR*, N°51549, Paris (in French).
- Franceschini N, Pichon JM, Blanès C (1992) From insect vision to robot vision. *Philosophical Transactions of the Royal Society London B* 337: 283-294
- Franceschini N, Kirschfeld K, Minke B (1981a) Fluorescence of photoreceptor cells observed in vivo. *Science* 213 : 1264-1267
- Franceschini N, Hardie RC, Ribi W, Kirschfeld K (1981b) Sexual dimorphism in a photoreceptor. *Nature* 291: 241-244
- Franceschini N, Riehle A, Le Nestour A (1989) Directionally selective motion detection by insect neurons. In: DG Stavenga and RC Hardie (eds.) *Facets of Vision*, Berlin, Springer, pp. 360-390.
- Franceschini N, Ruffier F, Serres J (2007). A bio-inspired flying robot sheds light on insect piloting abilities. *Current Biology* 17: 329-335
- Franceschini N, Ruffier F, Viollet S, Boyron, M (2003) Steering aid system for altitude and horizontal speed, perpendicular to the vertical, of an aircraft, and aircraft equipped therewith. *International Patent* PCT/FR2003/002611
- Frye M, Dickinson M (2001) Fly flight: A model for the neural control of complex behavior. *Neuron* 32 : 385–388
- Garratt MA, Chahl JS (2008). Vision-based terrain following for an unmanned rotorcraft. *Journal of Field Robotics* 25 : 284-301
- Gibson, JJ (1950) *The perception of the visual world*, Boston: Houghton Mifflin
- Gibson JJ, Olum P, Rosenblatt F (1955) Parallax and perspective during aircraft landings. *American Journal of Psychology* 68, 372-395
- Giurfa M (2003) The amazing mini-brain : lessons from a honeybee. *Beeworld* 84 : 5-18
- Giurfa M, Menzel R (1997) Insect visual perception: complex ability of simple nervous systems. *Current Opinion in Neurobiology* 7: 505–513
- Hardie RC (1985) Functional organization of the fly retina. *Progress in Sensory Physiology* 5, Ottosson D. (ed.), Springer, Berlin, pp. 2-79
- Hassenstein B, Reichardt W (1956) Systemtheoretische Analyse der Zeitreihenfolgen und Vorzeichenauswertung bei der Bewegungsperzeption des Rüsselkäfers *Chlorophanus*. *Zeitschrift für Naturforschung* 11b: 513-524
- Hausen K (1993) Decoding of retinal image flow in insects. In : FA Miles and J Wallman (eds.) *Visual motion and its role in the stabilization of gaze*, Amsterdam : Elsevier pp. 203-235
- Hausen K, Egelhaaf, M (1989) Neural mechanisms of course control in insects. In: DG Stavenga, RC Hardie (eds.), *Facets of vision*. Berlin, Springer pp. 391-424
- Heran P, Lindauer M (1963) Windkompensation und Seitenwindkorrektur der Bienen Flug über Wasser. *Zeitschrift für vergleichende Physiologie* 47 : 39-55
- Heisenberg M, Wolf R (1984) *Vision in Drosophila*. Berlin, Springer.
-

- Humbert JS, Hyslop AM (2010) Bioinspired visuomotor convergence. *IEEE Trans on Robotics* 26: 121-130
- Ibbotson MR (2001) Evidence for velocity-tuned motion-sensitive descending neurons in the honeybee. *Proceedings of the Royal Society, London B* 268: 2195-2201
- Kennedy JS (1939) Visual responses of flying mosquitoes. *Proceedings of the Zoological Society of London* 109 : 221-242
- Kennedy JS (1951) The migration of the desert locust (*Schistocerca gregaria* Forsk.) I. The behaviour of swarms. *Phil. Transactions of the Royal Society, London, B* 235 : 163-290
- Kirchner WH, Srinivasan MV (1989) Freely moving honeybees use image motion to estimate distance. *Naturwissenschaften* 76: 281-282
- Kirschfeld K (1967) Die Projektion der optischen Umwelt auf das Raster der Rhabdomere im Komplexauge von *Musca*. *Experimental Brain Research* 3: 248-270
- Kirschfeld K, Franceschini N (1968) Optische Eigenschaften der Ommatidien im Komplexauge von *Musca*. *Kybernetik* 5 : 47-52
- Kirschfeld K, Franceschini N, Minke B (1977) Evidence for a sensitizing pigment in fly photoreceptors, *Nature* 269 : 386-390
- Koenderink JJ (1986) Optic flow *Vision Research* 26, pp. 161-79
- Kramer J, Sarpeshkar R, Koch C (1995) An analog VLSI velocity sensor. In Proceedings of IEEE International symposium on Circuits and Systems, Seattle, USA, pp 413-416
- Krapp H, Hengstenberg B, Hengstenberg R (1998) Dendritic structure and receptive-field organisation of optic flow processing interneurons in the fly, *Journal of Neurophysiology* 79: 1902-1917.
- Laughlin S (1984). The role of parallel channels in early visual processing by the arthropod compound eye. In: MA Ali (ed.) *Photoreception and vision in invertebrates*. Plenum pp.457-481
- Lee DN (1980) The optic flow field: the foundation of vision. *Philosophical Transactions of the Royal Society London B* 290: 169-179
- Moeckel R, Liu SC (2007) Motion detection circuits for a time-to-travel algorithm. *Proceedings IEEE Int. Symposium Circuits and Systems (ISCAS07)*, pp. 3079-3082
- Mura F, Franceschini N (1994) Visual control of altitude and speed in a flying agent. In : D. Cliff et al. (eds), *From Animals to Animats III*, Cambridge: MIT Press, pp. 91-99
- Netter T, Franceschini N (1999) Neuromorphic optical flow sensing for nap-of-the-Earth flight. In : D Gage, H Choset (eds) *Mobile Robots XIV*, SPIE, Vol. 3838, pp. 208-216
- Netter T, Franceschini N (2002) A robotic aircraft that follows terrain using a neuromorphic eye. In : *Proceedings of the IEEE International Conference on Intelligent Robots and Systems (IROS)* Lausanne, Switzerland, pp. 129-134
- Pichon JM, Blanès C, Franceschini N (1989) Visual guidance of a mobile robot equipped with a network of self-motion sensors. In : WJ Wolfe, WH Chun (eds.) *Mobile Robots IV*, Bellingham, U.S.A : SPIE, Vol. 1195, pp. 44-53
- Portelli G, Serres J, Ruffier F, Franceschini N (2008) An Insect-Inspired Visual Autopilot for Corridor-Following. *Proceedings of the 2nd Biennial IEEE Int. Conference on Biomedical Robotics and Biomechatronics*, BioRob 08, Scottsdale, USA, pp. 19-26
- Portelli G, Ruffier F, Franceschini N (2010a) Honeybees change their height to restore their optic flow. *J. Comp. Physiol. A* (in press, DOI :10.1007/s00359-010-0510-z)
- Portelli G, Serres J, Ruffier F, Franceschini N (2010b) Modelling honeybee visual guidance in a 3-D environment *J. Physiol. Paris*, 104: 27-39
- Preiss R (1992) Set point of retinal velocity of ground images in the control of swarming flight of desert locusts. *Journal Comparative Physiology A* 171 : 251-256
-

- Pudas M, Viollet S, Ruffier F, Kruusing A, Amic S, Leppävuori S, Franceschini N (2007) A miniature bio-inspired optic flow sensor based on low temperature co-fired ceramics (LTCC) technology, *Sensors and Actuators A* 133 : 88-95
- Reichardt W (1969) Movement perception in insects. In: W. Reichardt (ed.) *Processing of Optical Data by Organisms and by Machines*, New York: Academic Press, pp. 465-493
- Riehle A, Franceschini N (1984) Motion detection in flies: parametric control over ON-OFF pathways. *Experimental Brain Research* 54 : 390-394
- Riley JR, Osborne JL (2001) Flight trajectories of foraging insects: observations using harmonic radar. In: TP Woïwod, DR Reynolds, CD Thomas (eds.) *Insect movement: Mechanisms and consequences* CAB International, pp. 129-157
- Rossel S, Wehner R (1984) How bees analyze the polarization pattern in the sky. Experiments and model. *J. Comp. Physiol.* A154 : 607-615
- Ruffier F, Franceschini N (2003) OCTAVE, a bioinspired visuo-motor control system for the guidance of Micro-Air Vehicles, In: A Rodriguez-Vazquez et al. (eds.) *Bioengineered and Bioinspired Systems*, Bellingham, U.S.A, SPIE, Vol. 5119, pp.1-12
- Ruffier F, Franceschini N (2004a) Visually guided micro-aerial vehicle: automatic take-off, terrain following, landing and wind reaction. *Proceedings IEEE International Conference on Robotics and Automation (ICRA04)*, New Orleans, USA, pp. 2339-2346
- Ruffier F, Franceschini N (2004b) Optic flow based AFCS for rotorcraft automatic maneuvering (terrain following, takeoff and landing). *Proceedings of the 30th European Rotorcraft Forum, AAF/CEAS*, Marseille, 71.1-71.9.
- Ruffier F, Franceschini N (2005) Optic flow regulation: the key to aircraft automatic guidance. *Robotics and Automomous Systems* 50 : 177-194
- Ruffier F, Viollet S, Amic S, Franceschini N (2003) Bio-inspired optical flow circuits for the visual guidance of micro-air vehicles. *Proceedings the IEEE International Symposium on Circuits and Systems (ISCAS)*, Bangkok, Thailand, Vol.III, pp. 846-849
- Santos-Victor J, Sandini G, Curotto F, Garibaldi S (1995) Divergent stereo in autonomous navigation: from bees to robots. *International J. of Computer Vision* 14: 159-177
-
- Serres J, Masson G., Ruffier F, Franceschini N (2008a) A bee in the corridor : centring and wall following. *Naturwissenschaften*, 95 : 1181-1187
- Serres J, Dray, D, Ruffier F, Franceschini N (2008b) A vision-based autopilot for a miniature air vehicle: joint speed control and lateral obstacle avoidance. *Autonomous Robots* 25: 103-122
- Shoemaker PA, O'Carroll DC, Straw AD (2005) Velocity constancy and models for wide-field visual motion detection in insects. *Biological Cybernetics*, 93 : 275-287
- Srinivasan MV (1993) How insects infer range from visual motion. In : FA Miles, J Wallman (eds.) *Visual motion and its role in the stabilization of gaze*. Amsterdam : Elsevier, pp.139-156
- Srinivasan M, Thurrowgood S, Soccol D (2006) An optical system for guidance of terrain following in UAVs. *Proceedings of the IEEE International Conference on video and signal based surveillance AVSS06*
- Srinivasan MV, Lehrer M, Kirchner WH, Zhang, SW(1991) Range perception through apparent image speed in freely flying honeybees. *Visual Neuroscience* 6: 519-535

- Srinivasan, MV, Zhang SW, Chandrashekara K (1993) Evidence for two distinct movement-detecting mechanisms in insect vision. *Naturwissenschaften* 80: 38-41
- Srinivasan MV, Zhang SW, Lehrer M Collett T (1996) Honeybee navigation en route to the goal: visual flight control and odometry. *Journal of Experimental Biology* 199: 237-244
- Srinivasan MV, Zhang SW, Chahl JS, Barth E, Venkatesh S (2000) How honeybees make grazing landings on flat surface. *Biological Cybernetics* 83: 171-183
- Srygley RB, Oliveira EG (2001) Orientation mechanisms and migration strategies within the flight boundary layer. In: TP Woiwod, DR Reynolds and CD Thomas (eds.) *Insect movements: mechanisms and consequences*, CAB international, pp. 183-206
- Strausfeld NJ (1976) *Atlas of an insect brain*, Springer: Berlin
- Straw AD, Rainsford T, O'Carroll DC (2008) Contrast sensitivity of insect motion detectors to natural images. *Journal of Vision* 8: 1-9
- Taylor GK, Krapp HG (2008) Sensory systems and flight stability : what do insects measure and why ? In : J. Casas and S.J. Simpson (eds.) *Advances in Insect Physiol. 34 : Insects mechanisms and control*, Amsterdam : Elsevier, pp. 231-316
- Ullman S (1981) Analysis of visual motion by biological and computer systems, *Computer* 14 : 57-69
- Valette F, Ruffier F, Viollet S, Seidl, T (2010) Biomimetic optic flow sensing applied to a lunar landing scenario. *Proc. IEEE Intern. Conf. Robotics and Automation*, Anchorage, 2010 (in press)
- Webb B (2001) Can robots make good models of biological behavior ? *Behavioral and Brain Sciences* 24 : 6
- Whiteside TC, Samuel GD(1970) Blur zone. *Nature* 225 : 94-95
- Zettler F, Weiler R (1974) Neuronal processing in the first optic neuropile of the compound eye of the fly. In: F. Zettler and R. Weiler (eds.) *Neural principles in vision*, Berlin, Springer, pp. 226-237
- Zufferey JC (2008) *Bio-inspired flying robots*, Boca Raton, EPFL Press/CRC Press