# Chapter 1

# Experimental Approaches Toward a Functional Understanding of Insect Flight Control

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**Abstract** This chapter describes experimental approaches exploring free-flight control in insects at various levels, in view of the biomimetic design principles they may offer for MAVs. Low-level flight control is addressed with recent studies of the aerodynamics of free-flight control in the fruit fly. The ability to measure instantaneous kinematics and aerodynamic forces in free-flying insects provides a basis for the design of flapping airfoil MAVs. Intermediate-level flight control is addressed by presenting a behavioral system identification approach. In this work, the motion processing and speed control pathways of the fruit fly were reverse engineered based on transient visual flight speed responses, providing a quantitative control model suited for biomimetic implementation. Finally, high-level flight control is addressed with the analysis of landmark-based goal navigation, for which bees combine and adapt basic visuomotor reflexes in a context-dependent way. Adaptive control strategies are also likely suited for MAVs that need to perform in complex and unpredictable environments. The integrative analysis of flight control mechanisms in free-flying insects promises to move beyond isolated emulations of biological subsystems toward a generalized and rigorous approach.

## 1.1 Introduction

Flying insects achieve efficient and robust flight control despite size constraints and hence limited neural resources [6, 12]. This is achieved from closely integrated and often highly specialized sensorimotor control pathways [19], making insects an ideal model system for the identification of biological flight control mechanisms, which can serve as design principles for future autonomous micro-air vehicles (MAVs) [18, 16, 38, 62]. While the implementation of biomimetic design principles in MAVs and other technical devices is inherently appealing, such an approach has its pitfalls that can easily lead to misconceptions [54].

A first problem relates to the immense complexity of biological systems, in particular flight control mechanisms. The multimodal sensorimotor pathways represent a high-dimensional control system, whose function and underlying physiology are understood only partially. A second problem relates to the often substantially different spatial and temporal scales of insects and MAVs. A meaningful transfer of a control mechanism identified in a small insect to its typically much larger robotic counterpart is non-trivial and requires detailed knowledge of the system dynamics. For example, it is not obvious how to control a robot based on motion processing principles derived from insects [41, 62], which perform maneuvers much faster and based on completely different locomotion principles than their robotic counterparts.

This chapter presents recent experimental approaches aimed at a functional understanding of insect flight control mechanisms. To this end, flight control in insects is addressed at various levels, from the

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biomechanics of flapping flight to flight control strategies and high-level navigational control. The experimental approaches share in common a detailed analysis of the time-continuous processes underlying the control of free flight under highly controlled and yet meaningful experimental conditions.

### 1.1.1 Chapter Overview

- **Low level: Biomechanics.** A formidable challenge for the design of MAVs is to generate sufficient aerodynamic forces to remain aloft, while controlling these forces to stabilize flight and perform maneuvers. The sensorimotor system of insects has evolved under size constraints that may be quite similar to those of MAVs. Consequently, the biological solutions enabling flight in these small animals may provide useful design principles for the implementation of MAVs.

  The first example in this chapter addresses low-level flight control with a detailed description of free-flight biomechanics in the fruit fly *Drosophila* [29, 30]. 3D high-speed videography and dynamical force scaling were combined to resolve the movements of the wings and the resulting aerodynamic forces. The time-resolved analysis reveals aerodynamic and control requirements of insect flight, which are likewise essential to MAV design [60, 17, 16, 58], also see Chaps. 11–16.

- **Intermediate level: Visuomotor reflexes.** To navigate autonomously in a cluttered environment, MAVs need to sense objects and produce appropriate responses, such as to avoid an impending collision. Insects meet this challenge with reflexive responses to the optic flow [33], i.e., the perceived relative motion of the environment during flight. The so-called optomotor reflexes mediate various visual flight responses, including attitude control, collision avoidance, landing, as well as control of heading, flight speed, and altitude. Optomotor reflexes provide a powerful model system to explore visual processing and flight control principles, reviewed in [12, 21, 46, 50], also see Chaps. 2, 4, and 17.

  The second example in this chapter describes a rigorous system analysis of the fruit fly's visual flight speed response using *TrackFly*, a wind tunnel equipped with virtual reality technology [27]. The identification of the control dynamics in the form of a controller provides a powerful strategy to transfer biological control principles into the robotic context, including MAVs [17, 16], also see Chap. 3.

- **High level: Landmark navigation.** Autonomous MAVs should ultimately be able to flexibly solve meaningful tasks, such as navigate through cluttered, unpredictable, and potentially dangerous environments, and safely return to their base. Here, too, insects can serve as a model system, as some species show the impressive ability to acquire the knowledge of specific locations in their environment (e.g., nest, food site), which they repeatedly visit over the course of many days [56], also see Chaps. 2 and 7.

  The third example in this chapter describes an experimental approach aimed to explain landmark-based goal navigation in honey bees from a detailed analysis of individual maneuvers. Goal navigation is explained with basic sensorimotor control mechanisms that are combined and modified through the learning experience. The ability to achieve robust, adaptive, and flexible flight control as an emergent property of basic sensorimotor control principles offers yet more interesting options for the design of autonomous MAVs with limited built-in control circuits.

## 1.2 Low-Level Flight Control – Biomechanics of Free Flight

A detailed knowledge of flight biomechanics provides the foundation for our understanding of biological flight control strategies – or their implementation in MAVs. Flight control is ideally studied in free flight, in which the natural flight behavior of an insect can be measured under realistic sensory and dynamic flight conditions. To understand how a flapping insect stabilizes its flight and performs maneuvers, the underlying mechanisms must be studied at the level of single wing strokes – not an easy task, considering the tiny forces and short timescales involved.

The example described in this section shows how the application of 3D high-speed videography and dynamic force scaling using a robotic fly wing allowed such a detailed analysis of free-flight biomechanics to

be performed in the fruit fly *Drosophila*, a powerful model system for the design of flapping airfoil MAVs [18, 17, 16, 58].

## 1.2.1 Research Background

The aerodynamic basis of insect flight has remained enigmatic due to the complexities related to the intrinsically unsteady nature of flapping flight [57]. A solid theoretical basis for quantitative analyses of insect flight aerodynamics was provided by Ellington's influential theoretical work based on time-averaged models [22]. At the experimental level, dynamically scaled robotic wings provided the technological breakthrough allowing aerodynamic effects to be explored empirically at the timescale of a single wing stroke [44].

## 1.2.2 Experiments

To perform a time-resolved biomechanical analysis of free flight, the wing and body movements of fruit flies were recorded using 3D high-speed videography (Fig. 1.1A). For this, hungry flies were released into a small flight chamber (side length 30 cm). Attracted by a black cylindrical cup filled with vinegar, the flies approached the center of the chamber, where they often hovered before landing on the cup or instead performed a fast turning maneuver (saccade) in order to avoid colliding with it. These flight sequences were filmed using three orthogonally aligned high-speed cameras, whose lines of sight intersected in the middle of the flight chamber.

Next, the wing and body kinematics were extracted using a custom-programmed graphical user interface (Fig. 1.1B). The wing kinematics were then played through a dynamically scaled robotic wing (*Robofly*, Fig. 1.1C) to measure the aerodynamic wing forces (arrows in Fig. 1.1B) throughout the filmed flight sequence. Combining the kinematic and force data allowed a direct calculation of instantaneous aerodynamic forces, torques, and power (see below).

### 1.2.2.1 Hovering Flight

Hovering flight offers itself for an analysis of the aerodynamic requirements of flapping flight without the complications resulting from body motion. The analysis of such a hovering sequence, consisting of six consecutive wing strokes, is shown in Fig. 1.2. The precisely controlled wing movements are characterized by a high angle of attack and maximal force
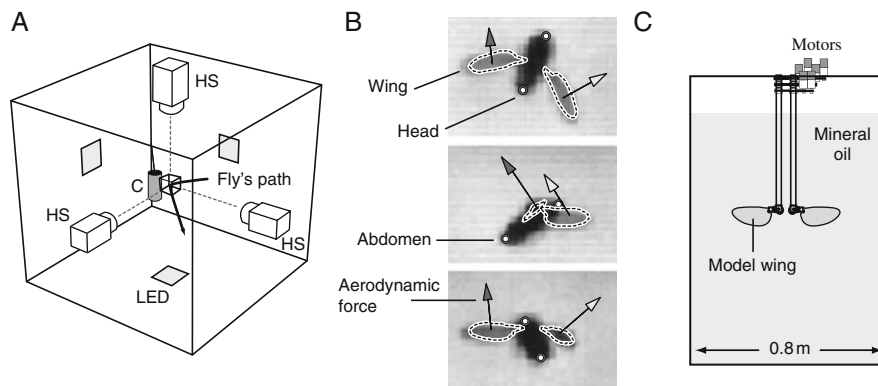


**Fig. 1.1** Measurement of kinematics and forces. (**A**) Setup: Flies were filmed with three orthogonally aligned high-speed (5000 fps) cameras (HS). Arrays of near-infrared light emitting diodes (LEDs) were used for back-lighting. Flies were attracted to a small cylindrical cup (C), in front of which they were filmed within the small overlapping field of view of the cameras (shown as a wire-frame cube). (**B**) Kinematic extraction: Wing and body kinematics were measured using a graphical user interface, which allowed a user to match the wing silhouettes and the positions of the head and abdomen to obtain their 3D positions. *Arrows* show the aerodynamic forces measured using *Robofly*. (**C**) "Robofly": Plexiglas wings (25 cm in length) were flapped in mineral oil at the appropriate frequency to match the Reynolds number of the fly's flapping wings in air (and hence the fluid dynamics). The up-scaled fluid dynamic forces were measured with strain gauges on the wings and the aerodynamic forces acting on the fly's wings (shown in **B**) were back-calculated. Figure modified from [30]
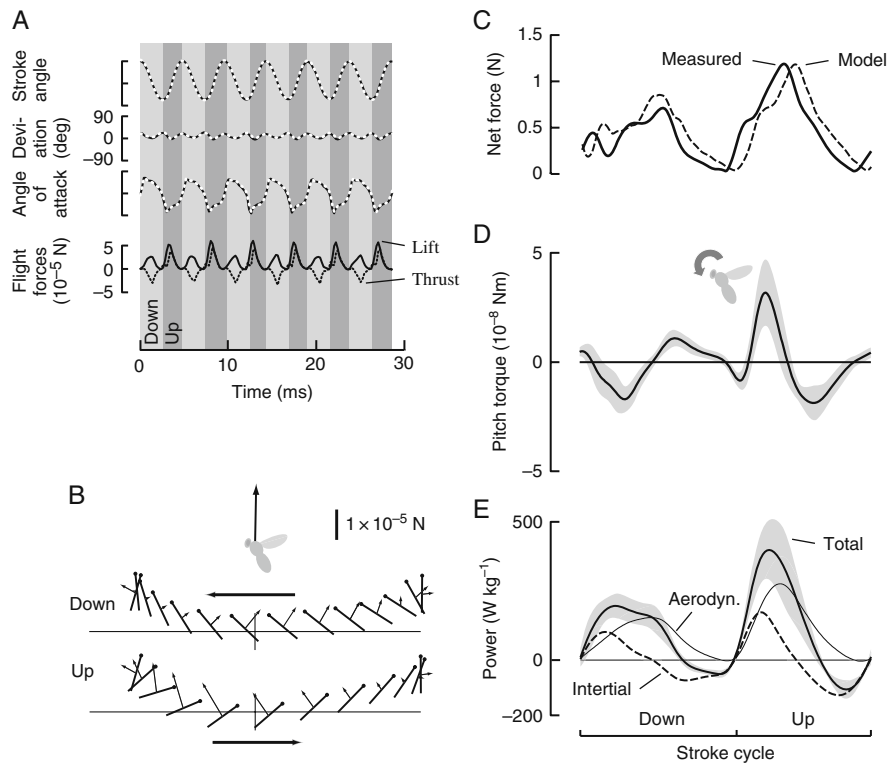
**Fig. 1.2** Hovering flight. (**A**) Wing kinematics and flight forces. Data from six consecutive wing beats are shown. For a definition of the stroke angles refer to [30]. (**B**) Wing motion and forces. Successive wing positions during a hovering stroke cycle are shown with matchstick symbols (*dots* show the leading edge). Instantaneous aerodynamic forces are shown with *arrows*. Axes indicate horizontal (± 90°) and vertical (± 10°) stroke positions. The *arrow* shown with the fly shows the aerodynamic force averaged over the stroke cycle. (**C**) Quasi-steady analysis of instantaneous aerodynamic force. The measured force is shown together with the force predicted by a quasi-steady model [20]. (**D**) Instantaneous pitch torque. Pitch torque (*black line* ± S.D.) oscillates around a mean of zero during hovering. (**E**) Instantaneous specific flight power (in W/kg muscle mass). Traces show total mechanical power (±S.D.), which is composed of the aerodynamic and inertial power required for wing motion. Figure modified from [30]

production during the middle of the downstroke and the early upstroke (Fig. 1.2A, B). As expected for hovering, the drag of the downstroke and upstroke cancels itself out, while the mean lift offsets the fly's weight. The aerodynamic forces generated by the wing movements are largely explained with a quasi-steady model that takes into account translational and rotational effects of the wing motion (Fig. 1.2C). The main discrepancy between the modeled and measured forces is a phase delay, which is likely due to unsteady effects (e.g., wing–wake interactions) not considered here.

A further requirement of stable hovering flight is a precise balance of the aerodynamic torques over the course of a wing stroke. To maintain a constant body pitch, for example, the substantial torque peaks generated throughout the stroke cycle must cancel each other out precisely, as shown in Fig. 1.2D. Finally, the instantaneous power was calculated directly from the scalar product of wing velocity and the forces acting on the wings (Fig. 1.2E). The power associated with aerodynamic force production peaks around the middle of each half-stroke, when aerodynamic forces and wing velocity are maximal. Conversely, the power required to overcome wing inertia reverses its sign during each half-stroke due to the deceleration of the wings toward the end of each half-stroke. The total mechanical power, the sum of these two components, is positive for most part of the wing stroke. Power is negative when the wings decelerate while producing little aerodynamic force, which occurs briefly toward

the end of each half-stroke. During this phase, the mechanical power could be stored elastically and partially retrieved during the subsequent half-stroke to reduce the total power requirements. The potential reduction of flight power in fruit flies, however, is quite limited (in the order of 10%).

### 1.2.2.2 Maneuvering

This approach was taken further to explore how flies modify their wing kinematics during flight maneuvers. Flight sequences containing saccadic turning maneuvers were filmed and the aerodynamic wing forces again measured using *Robofly*. Figure 1.3A shows wing tip trajectories during such maneuvers, labeled according to the yaw torque they produced. At the onset of a turn, the outside wing tilts backward and its amplitude increases (light gray tip trajectories). Conversely, the inside wing tilts forward and its amplitude decreases (dark gray trajectories). The resulting difference in yaw torque generated by the two wings is sufficient to accelerate the fly to over 1000°/s within about five wing strokes [29]. The changes in stroke plane angle and stroke amplitude over the course of a saccade are shown in Fig. 1.3B. To maximally accelerate at the onset of the saccade, the difference in stroke amplitude between the outside and inside wing is only around 5°, while the stroke plane angle differs by a mere 2°. Even during extreme flight maneuvers, therefore, the changes in wing kinematics are quite small.

### 1.2.3 Conclusions

The physical constraints may be similar for MAVs and flies operating at similar size scales, and the flight control mechanisms evolved in insects can therefore provide valuable design principles for MAVs. The application of high-speed videography and aerodynamic force measurements using dynamically scaled robots provides detailed insights into the requirements of insect flight control that can help identify important design constraints for MAVs.

This analysis reveals critical aspects of flight control in *Drosophila* that need to be considered also for MAV design. Precise and fast wing actuation appears most critical for flight control. As shown by the example of pitch torque, the instantaneous torques produced by the wings vary considerably and must be precisely balanced over the course of a stroke cycle. As shown by the analysis of yaw torque during turning maneuvers, even subtle changes in wing motion are sufficient to induce fast turns within a few wing beats. Precise and fast sensorimotor control loops are obviously required for flight control using similar morphologies.

The experiments also indicate less critical features of flapping flight control, at least at the size scale of the fruit fly. Wing stiffness and surface structure, for example, may be relatively unimportant under certain conditions. The simple Plexiglas wing used in *Robofly* was sufficient to reproduce the required aerodynamic forces without the need to mimic the quite complicated structure of the fly's wing. The feasibility of a stiff,
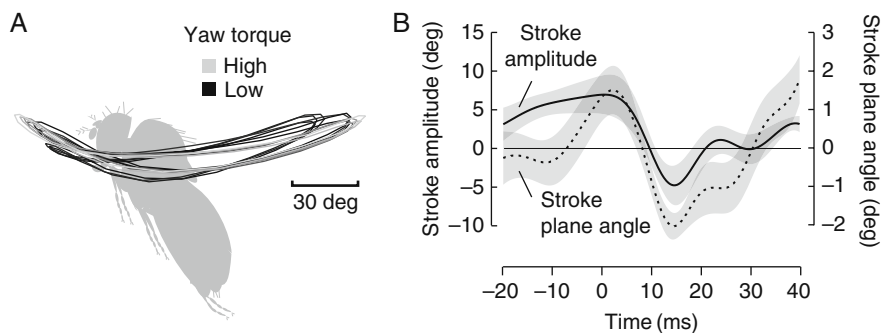


**Fig. 1.3** Maneuvering. (**A**) Changes in wing kinematics associated with yaw torque production during saccades. Wing tip trajectories were measured during free-flight turning maneuvers (saccades). Wing tip trajectories associated with high and low aerodynamic yaw torques are shown as *light* and *dark gray lines*, respectively. (**B**) Bilateral changes in wing kinematics during a turning maneuver. At the onset of a turn, the outside wing increases the stroke amplitude and stroke plane angle (backward tilt) relative to the inside wing. Figure modified from [29]

light-weight wing structure for flapping lift production was recently demonstrated in [59]. As a further simplification, quasi-steady mechanisms of aerodynamic force production dominate in the production of aerodynamic forces of flapping wings, at least in the fruit fly. Unsteady effects, such as wing–wing and wing–wake interactions, play a minor role, such that simple analytical tools can be applied at least in first approximation. Finally, elastic storage plays a comparatively small role given the small mass of the wings, and therefore does not present a significant design constraint.

In conclusion, the measurement of instantaneous wing positions in free flight, together with the aerodynamic forces measured in the robotic wing, is sufficient to robustly quantify several relevant aspects of flight biomechanics. The example of the fruit fly, itself a powerful model for MAV design [61, 60], reveals a suitable strategy to get flapping MAVs off the ground. The next substantial challenge is to actively stabilize flight, for which exceedingly fast and precise wing control is required. The impressive advances in flight biomechanics provide a solid foundation for biomimetic MAV design that takes into account the requirement for flight control.

## 1.3 Intermediate-Level Flight Control – Visuomotor Reflexes

An intermediate level of flight control involves reflexive responses to sensory input. On the one hand, they can mediate corrective maneuvers to recover from disturbances and unstable flight conditions to increase dynamic system stability. On the other hand, they can mediate flight maneuvers to suitably respond in an unpredictable environment. For example, an MAV equipped with motion sensors can sense an object appearing in front and respond with an avoidance maneuver to prevent a collision. Equipped with the appropriate sensors and flight control strategies, autonomous MAVs can navigate more safely and efficiently within cluttered and unpredictable environments (Chaps. 3 and 8).

The extremely efficient and robust visuomotor reflexes of insects can provide design principles for biomimetic flight control strategies in autonomous MAVs. The second part of this chapter describes behavioral experiments aimed at a rigorous system identification of visuomotor control pathways in the fruit fly. The characterization of biological control pathways in the form of a control model allows more direct and meaningful transfer of biological flight control principles into a robotic context, including MAVs [17, 16].

### 1.3.1 Research Background

Pioneering experiments explored the transfer properties of optomotor turning reflexes in insects. This was achieved with a simple preparation, in which insects were stimulated using a rotating drum and their intended turning responses measured using elegant techniques [36, 23, 34]. The response tuning of optomotor turning reflexes provides the foundation for a cohesive theory of optic flow processing in insects to this day, reviewed in [6, 4, 37, 5], also see Chaps. 4 and 5.

While tethering provides a simple method to deliver stimuli without influence of the behavioral reactions (referred to as *open loop* in the biological literature), the results of such experiments are difficult to interpret functionally [49]. Tethering disrupts various reafferent feedback circuits, which leads to significant behavioral artifacts [30] and prevents the analysis of flight control under realistic dynamical conditions.

Visual reflexes have also been extensively explored in free flight, reviewed in [12, 6, 46], in which case the visual input is coupled to the insect's flight behavior (natural *closed-loop* condition) [45, 49]. This coupling hinders a rigorous system identification because the stimuli are no longer under complete experimental control. Nevertheless, data obtained in this way can provide valuable insight into flight control mechanisms [40, 11, 3], Chap. 2. A simpler behavioral analysis becomes possible from measuring free-flight behavior under steady-state conditions [15, 47, 2], but cannot address questions relating to flight control dynamics.

### 1.3.2 Experiments

A functional understanding of biological flight control principles that can be meaningfully transferred into MAVs requires careful consideration of the

multimodal reafferent pathways. Below I describe a recent experimental approach aimed at a system identification of visuomotor pathways that can serve as design principles for MAV control.

### 1.3.2.1 System Analysis of Visual Flight Speed Control Using Virtual Reality Display Technology

To perform a system identification of the fruit fly's motion-dependent flight speed control pathways, a wind tunnel was equipped with virtual reality display technology (*TrackFly* [27], Fig. 1.4).

An automated procedure was implemented to induce flies to fly to the center of the wind tunnel and then stimulate them with horizontally moving sine gratings of defined temporal frequency (TF), spatial frequency (SF), and contrast. To hold the linear image velocity (defined as TF/SF) constant in the fly's eyes, the grating speed was adjusted continuously to compensate for the displacement of the fly (one-parameter open-loop paradigm). The automated high-throughput system allowed a large data set of visual responses to be measured for a broad range of temporal and spatial frequencies. The results show that fruit flies



**Fig. 1.4** TrackFly. A wind tunnel was equipped with a virtual reality display system (only working section of the wind tunnel is shown). Visual stimuli were presented to free-flying flies in open loop, i.e., the pattern offset was adjusted to the fly's position along the wind tunnel in real time. M: Mirror; LP: Light path; Cam: Video camera. For details see [27]

respond to the linear velocity (TF/SF) of the patterns, which serves as a control signal for flight speed [27]. The visual tuning properties of visual flight speed responses differ from optomotor turning responses, which instead show a response maximum at a particular temporal frequency (TF) of displayed patterns [34].

Next, system identification procedures were applied to obtain a controller that was able to reproduce the transient open-loop response properties, i.e., reproduce the transient changes in flight speed after onset of the optic flow stimulus. The controller was then used to predict the speed responses under more realistic visual closed-loop conditions, and the results confirmed with data obtained from flies tested in closed loop. A detailed quantitative account of the procedures and data is published elsewhere ([27], [28], Rohrseitz and Fry, in prep.).

### 1.3.3 Conclusions

The reflexive flight control pathways of insects can provide powerful control architectures for biomimetic MAVs. For a meaningful interpretation of the biological measurements, however, the behavioral context and relevance of multimodal feedback must be carefully considered. Free-flight experiments are ideal to explore flight control under realistic flight conditions, but the difficulty of delivering arbitrary stimuli in a controlled manner is a hindrance for detailed behavioral system identification.

The described approach works around this limitation by allowing a particular parameter (here: pattern speed) to be presented in open loop, without disrupting the remaining stimuli. From the measured transient responses, linear pattern velocity was identified as the relevant control parameter for visual flight speed control. Based on this high-level understanding, the underlying visual computations and neural structures can be further explored.

Next, the transient responses were used to reverse engineer the control scheme underlying flight speed control (Fig 1.5). The measurements performed in open and closed loop are quantitatively explained by a proportional control law, which is simpler still than a PID controller recently suggested for insects [24], Chap. 3.

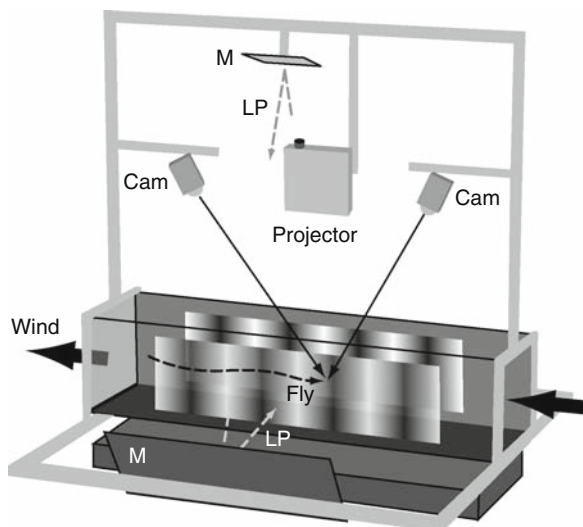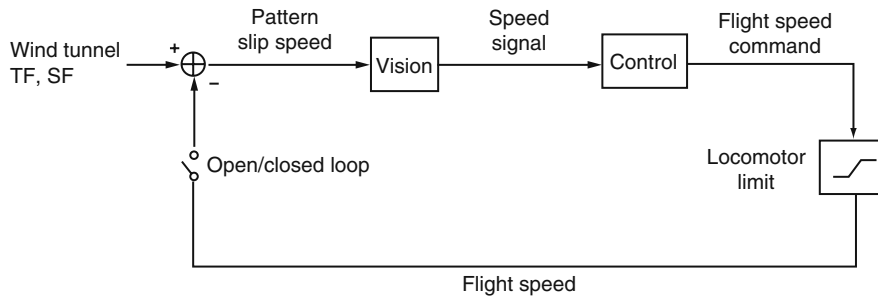A rigorous system identification approach in biology provides a functional understanding of the

**Fig. 1.5** Control model. The fly's flight speed responses are quantitatively explained by a simple control model. The visual system computes pattern velocity as input to a controller of flight speed, which is constrained by measured locomotor limits. The simulated flight speed responses in open and closed loop (note switch symbol) were verified experimentally using *TrackFly*

underlying neuromotor pathways and characterizes their dynamics in a concrete control model. The control strategy can then be meaningfully transferred into MAVs even if the underlying neuromotor mechanisms remain only partially known.

## 1.4 High-Level Flight Control – Landmark-Guided Goal Navigation

High-level flight control strategies are ultimately required to enable MAVs to perform meaningful tasks, for which sensory input must be processed in a context-dependent way. For example, an MAV could rely on the same visual objects encountered along its flight path during the outbound trip and to return to its home base, requiring a context-dependent processing of the visual input.

Some insect species reveal the amazing ability to return to quite distant places that they previously visited. Honey bees, for example, learn the location of a rewarding food source, which they repeatedly visit to collect food for the hive (also see Chaps. 2 and 7). The third example of this chapter describes experiments exploring the basic control principles underlying such complex, context-dependent behaviors.

Landmark-based goal navigation is explained with visuomotor control mechanisms that are modified through learning experience. Complex flight behaviors result as an emergent property of basic flight control strategies and their interactions with the environment. Similar control strategies could allow MAVs with limited resources to likewise perform well in complex, real-world applications.

### 1.4.1 Research Background

The mechanisms by which flying insects use landmarks to return to a learned place was pioneered by Tinbergen's (1932) [52] classic neuroethological studies in the digger wasp. His approach, followed by many later researchers (e.g., for flying honey bees [1, 7]; review [55]), was to induce search flights in experimentally modified visual surroundings and conclude from the search location the internal visual representation of the visual environment.

A similar approach in honey bees performed half a century later led to the influential *snapshot model* [8], which explained goal-directed flight control to result from a comparison between the current retinal image and a template image formerly stored at the goal location. The ways in which insects represent locations as visual memories and use these to return to a learned place are studied experimentally in increasing detail, see recent reviews in [13, 10]. Not least due to its algorithmic formulation, the snapshot and related models found widespread appeal in the robotic community and were further explored in numeric [43] and robotic [39, 42] implementations, reviewed in [25, 53].

### 1.4.2 Experiments

The experiments giving rise to the snapshot model were first replicated and extended to explore landmark-based goal navigation in more detail [31]. The results were suggestive of alternative visuomotor control strategies, which were subsequently explored with detailed analyses of individual approach flights using more advanced video tracking techniques [26].
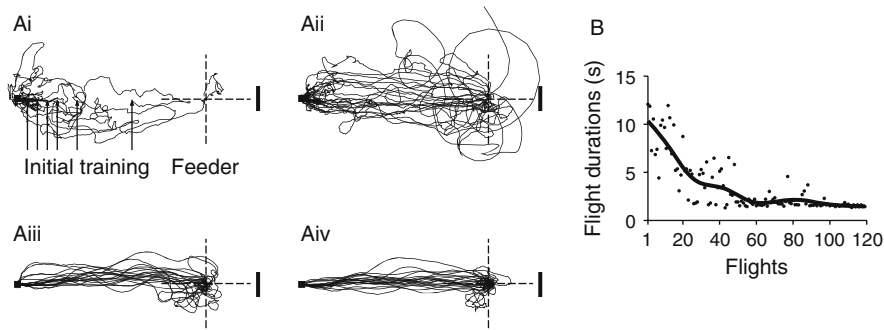
**Fig. 1.6** Learning experiments. (**A**) Successive approach flights of a single bee. The experiments were performed in a cylindrical tent (Ø 2.4 m). The bee entered on the left and flew to an inconspicuous feeder (location indicated with a stippled cross-hair) 0.5 m in front of a black paper square attached to the back wall (shown as a *black bar* on the *right*). (**i**) Initial training. The bee was trained by displacing a temporary feeder (location shown with *arrows*) closer toward the final feeder position on consecutive foraging trips. *Lines* show the flight trajectories toward the temporary and final feeder positions. (**ii**) Flights 1–20. (**iii**) Flights 51–70. (**iv**) Flights 101–120. (**B**) Duration of successive flights. With increasing experience, flight duration decreased to about 2 s after about 50 flights. Figure modified from [32]

Detailed measurements of approach flights of bees to a goal location were made, taking care not to disrupt their natural behavior. To explore the relevance of learning, every single approach flight of a single bee was measured (Fig. 1.6). By moving a temporary feeder stepwise through a uniform flight tent, the bee was trained to fly toward a permanent feeder located in front of a single landmark (Fig. 1.6 Ai). The approach flights of this inexperienced bee were slow and quite convoluted. The first 20 flights of the same bee with the permanent feeder were faster, but still revealed turns and loops reminiscent of search flights (Fig. 1.6 Aii). The bee's approaches became progressively faster and smoother as it gained experience during successive foraging trips (Fig. 1.6 Aiii). After about 100 flights, the bee approached the feeder with straight and fast trajectories. Duration of successive flights decreased from about 5–10 s to 2–3 s (Fig. 1.6B).

Next, individual bees were trained using landmark settings that differed in position, number, and color of the landmarks. First, a bee was trained with a single black cylinder (●) located just to the right of the feeder (Fig. 1.7A, left; feeder location is marked with cross-hairs). The bee approached the cylinder and performed occasional left turns, roughly aimed at the feeder position. During these approaches, the bee held the cylinder roughly in the frontal-right visual field (Fig. 1.7A, right). A different bee trained with the cylinder further to the right side still held the cylinder in the

right visual field and performed more convoluted flight paths toward the goal (Fig. 1.7B). In the identical situation, a second bee approached the feeder with a different approach pattern, but like the first bee held the cylinder in the right visual field (Fig. 1.7C).

This simple rule was even used by bees trained with two differently colored cylinders (marked L and R in Fig. 1.7D). The bees simply relied on one of the cylinders (in this case the right cylinder) for the initial approach, again holding it in the right visual field. The detailed structure of an approach flight, together with the measured body axis direction, is shown in (Fig. 1.7E).

These and other experiments provide a coherent view on the visuomotor strategies employed by bees to locate a goal in different environmental situations. Bees with little experience with a landmark setting (Fig. 1.6 Ai, Aii) or in the absence of a suitable (i.e., near-frontal) landmark (Fig. 1.7C) perform search-like flights. If a landmark is suitably located behind the goal (Fig. 1.6), an experienced bee will simply head toward it and find its goal. To do so, the bee needs to fixate the landmark in a frontal position, as symbolized with the curved arrows in Fig. 1.8A. If the bee tends to keep the landmark in the right visual field (Fig. 1.8B), it will tend to make turns to the left, as required for the final goal approach (Fig. 1.7). Finally, the bee can rely on one of several landmarks during its goal approach, if it associates it with the appropriate retinal position and/or turning direction (Fig. 1.8C). These results are
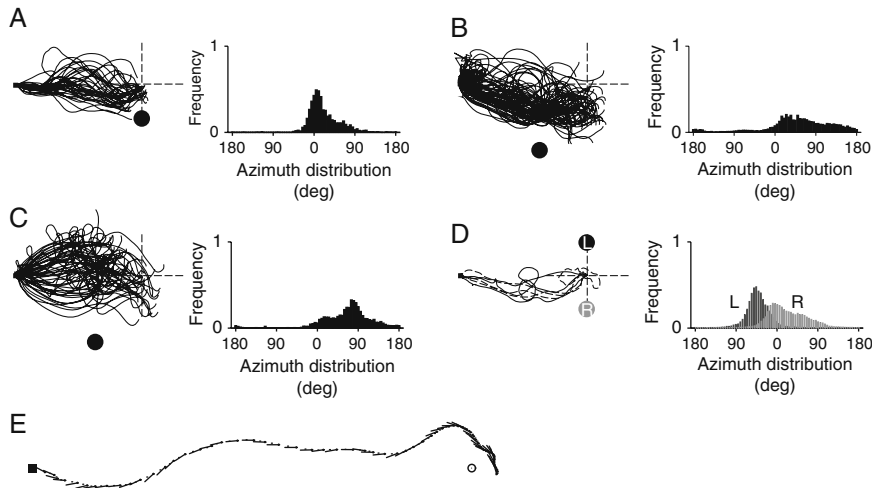
**Fig. 1.7** Approach flights and landmark azimuth during approach flights. (**A**) *Left*: 40 successive approach flights of an individual bee with a cylinder (•) positioned at an angular distance of 15° from the feeder (+). *Right*: Distribution of landmark positions in the bee's visual field. (**B**) Cylinder placed 40° to the right of the feeder. (**C**) As in (**B**), with data from a differ-ent bee. (**D**) Approach flights of two individual bees in the presence of two cylinders of different colors. The bees headed toward the right (R) cylinder. (**E**) Typical example of a bee's approach flight. The bee's position (*dots*) and body axis direction (*lines*) were measured at 50 Hz using a pan-tilt tracking system [26]. Data are subsampled for clarity. Figure modified from [32]
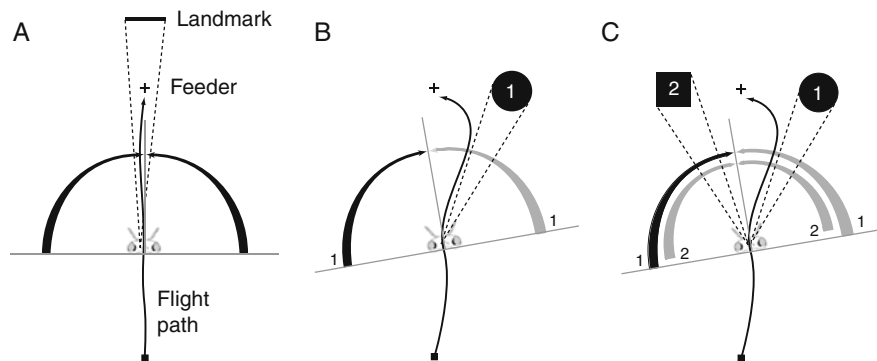


**Fig. 1.8** Visuomotor guidance model. (**A**) Frontal landmark. Bees fixate the landmark frontally. (**B**) Lateral landmark. Bees perform biased turns to the *left*, keeping the cylinder in the *right* visual field. (**C**) Two landmarks. Bees use one landmark dur-ing the approach. *Lines* show hypothetical flight paths. *Curved arrows* symbolize a learned visuomotor association. For details see [32]

consistent with various experiments performed in both flying and walking insects, e.g., [9, 35].

## 1.4.3 Conclusions

Landmark-based goal navigation in honey bees is explained as an emergent property of basic visuomotor reflexes, which are modified by a continuous learning process. Relatively unstructured, search-like flights are observed in bees with limited experience with the land-mark setting. A suitable landmark is used to direct the flight toward the goal, while successful flight motor patterns are reinforced by operant learning to increase the efficiency and reliability of the approach flights.

Control strategies based on a flexible and adapt-able employment of basic control loops may also be suited for MAVs with limited storage and processing capacity to enable successful landmark navigation. A

possible scenario could consist of exploring unfamiliar terrain and subsequently patrolling along suitable routes. The flexible use of comparatively basic visuomotor control strategies can more likely meet the high requirements for fast and robust flight control required by MAVs than a single complex and hard-wired algorithm. Flexible adaptation to varying environmental conditions and increasing experience provides a powerful strategy for flight control in complex and unpredictable environments.

## 1.5 Closing Words

Insects perform complex flight control tasks despite their small size and presumably limited neural capacity. The fact that insects nevertheless excel in their flight performance is explained with a close integration of specialized sensorimotor pathways.

While it is intriguing to take inspiration from flying insects for the design of autonomous MAVs, the high complexity of an insect's multimodal flight control system renders this task non-trivial and prone to misconceptions [54, 14, 50]. It may therefore be hardly fruitful – and indeed counter-productive – to take superficial inspiration from biology and implement the purported principles in robots without due care.

Instead, biologists and engineers should take advantage of the fact that insects can achieve superior flight control with possibly quite basic, but highly integrated control principles. To this end, detailed biological studies are required that address flight control mechanisms at various levels, including biomechanics, neural processing, sensorimotor integration, and high-level behavioral strategies. The experimental approaches described in this chapter show that advanced concepts and technologies can help provide the functional understanding of biological flight control principles required for meaningful biomimetic implementations in MAVs.

Not only can engineers profit from rigorous biological research of flight control, but the concepts and tools applied in engineering [17, 16] can likewise be meaningfully applied to explore biological control principles in a rigorous and quantitative way [51, 48, 49, 27]. The control principles thus identified in insects can then be transferred more easily into a robotic environment with appropriate consideration of the behavioral context and scaling issues.

The presented research examples motivate closer interactions between biological research of flight control mechanisms and engineering design of MAVs. Such interactions promise significant benefits to both fields, in that biologists can aim at more rigorous quantitative analyses of flight control and engineers can aim at more meaningful biomimetic implementations. Indeed, this aim will likely have been reached when the common fascination about flight control becomes the defining element of a coherent, interdisziplinary research effort.

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