

# Flight dynamics and control of evasive maneuvers: The fruit fly's takeoff

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**Abstract**—We have approached the problem of reverse engineering the flight control mechanism of the fruit fly by studying the dynamics of the responses to a visual stimulus during takeoff. Building upon a prior framework [1] we seek to understand the strategies employed by the animal to stabilize attitude and orientation during these evasive, highly dynamical maneuvers. As a first step, we consider the dynamics from a gray-box perspective: examining lumped forces produced by the insect's legs and wings. The reconstruction of the flight initiation dynamics, based on the unconstrained motion formulation for a rigid body, allows us to assess the fly's responses to a variety of initial conditions induced by its jump. Such assessment permits refinement by using a visual tracking algorithm to extract the kinematic envelope of the wings [2] in order to estimate lift and drag forces [3], and recording actual leg-joint kinematics and using them to estimate jump forces [4]. In this paper we present the details of our approach in a comprehensive manner including the salient results.

**Index Terms**—insect flight, takeoff dynamics, stability control.

## I. INTRODUCTION

**D**IFFICULTIES inherent to the miniaturization of unmanned aircraft have evoked studies of biological mechanisms for the development of innovative means of perception, actuation, and control [5], [6]. Particular interest has been put into characterizing insect flight, where these three components seem to interact quite effectively [7], [8]. This reverse engineering feat offers challenges that can be classified, roughly, into three major categories: modeling sensors and actuators, mapping variations of wing and body kinematics to the production of aerodynamic forces and moments, and understanding transformations from sensory input to changes in motor output.

While simplified aerodynamic models have given us acceptable estimates of the insect's production of forces and moments, other simplifications and assumptions limit a comprehensive understanding of insect flight

control. In the past, empirical assessments of the relation between wing and body kinematics, and the production of aerodynamic forces and moments have been made by studying hovering and steady forward flight. Under these conditions, plausible responses to small perturbations about the insect's desired operating point have been investigated. Naturally, this leads to two important questions: What occurs when the perturbations are not small? Does the insect consistently produce the same forces and moments to counteract these perturbations? These matters have been addressed to a certain extent by considering body saccades [9]. However, the framework presented here is aimed at extending these approaches to the full 6DOF case, with the underlying motivation of refining our current understanding of insect flight control.

We begin the analysis of highly dynamical maneuvers during takeoff by deriving reaction forces and moments from body-kinematic data [1]. In particular, we consider the voluntary takeoff dynamics as nominal responses, and investigate the perturbations observed in visually-elicited takeoffs. Once the 6DOF rigid body dynamics are characterized, we are able to consider the forces produced by the wings in response to the dynamics induced by the jump [3]. These forces can be estimated from wing-kinematic data, which have been extracted using a novel tracking algorithm [2] that utilizes a quaternion-based geometric model of the fly to capture the complex flapping motion. Finally, we are also able to investigate the initial flight conditions during takeoff by examining the role of the legs in providing initial forces [4]. This allows us to study the mechanisms used for control of directionality of the fly's trajectory at the onset of flight [10], and their overall impact on the fly's initial steadiness [3].

## II. FLIGHT INITIATION OF *Drosophila melanogaster*

Flying insects must transition between standing on the ground, and flying through the air, in a way that does not damage their wings [11]. To this end, the fruit

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fly's takeoff comprises a quick extension of the legs in tandem with a wing stroke. The latter, however, may or may not occur simultaneously with leg extension if the takeoff is elicited by a visual stimulus [1], [12] (Figure 1 and 2 illustrate this point). The differences of the fly's body kinematics following visually-elicited and voluntary takeoffs have been described previously [1]. This analysis clearly shows that visually-elicited escapes result in tumbling flights in which the insect translates faster, but also rotates rapidly around its three body-centered axes (Figure 2).



Fig. 1. Flight initiation in the absence of a visual stimulus. Simultaneous leg-extension and wing depression is observed in the center-top frame; the takeoff dynamics lead to “steady” flight.



Fig. 2. Flight initiation in response to visual stimulus. Typically, simultaneous leg-extension and wing depression does not occur (see center-top frame); the takeoff dynamics lead to “unsteady” flight.

#### A. From kinematics to dynamics: analysis of lumped forces and moments

Applying Newton's second law, we can substitute the body kinematics and determine the lumped reaction forces acting on the fly's body,

$$\begin{aligned}\mathbf{F}_T(t) &= m \dot{\mathbf{V}}(t) + \boldsymbol{\omega}(t) \times (m\mathbf{V}(t)) \\ \mathbf{M}_T(t) &= [\mathbf{I}] \dot{\boldsymbol{\omega}}(t) + \boldsymbol{\omega}(t) \times ([\mathbf{I}] \boldsymbol{\omega}(t)).\end{aligned}\quad (1)$$

Boldface notation is used to indicate vectorial quantities, and the overdot ( $\dot{\phantom{x}}$ ) is used to denote derivatives with respect to time.  $\mathbf{F}_T$  denotes the total force, which lumps the insect's weight, air resistance, leg forces, and wing forces,  $\mathbf{M}_T$  (another lumped quantity) denotes the net moment about the estimated center of mass,  $m$  denotes the mass of the fly,  $\mathbf{V}$  and  $\boldsymbol{\omega}$  denote the translational and rotational velocity vectors, respectively, and  $[\mathbf{I}]$  denotes the inertia tensor.

The reaction forces are shown in Figure 3. We observe that initially the forces generated during escape takeoffs exceed those during voluntary ones. Examining the differences between the two, we notice that in all voluntary takeoffs simultaneous leg extension and wing depression occurs. However, in some escape takeoffs the first wingbeat occurs after the middle legs lose contact with the substrate (Figure 2). Interestingly, the dynamics of escape takeoffs across different flies have similar magnitudes irrespective of when wing depression occurred. Thus, this suggests that the main difference during voluntary and escape takeoffs, in terms of the initial dynamics, relates to leg extension rather than wing depression. Consequently, leg forces play a crucial role in the steadiness of flight initiations, and wing forces do not seem sufficient to guarantee an initially steady takeoff during visually-elicited responses. Thus, a series of maneuvers must be performed by the fly to be able to reach forward flight at constant speed.

#### B. De-lumping flight forces and moments

From the unconstrained motion of the insect, we can parse the individual contributions of the legs and wings to determine the initial conditions for each takeoff sequence, and the corresponding responses used to achieve steady flight.

1) *Leg forces*: Using strain gauge measurements Zumstein *et al.* quantified through an isometric test the forces produced by the mesothoracic legs in *Drosophila* [14]. In addition, they derived through a kinetic analysis the forces generated by these insects during the course of leg extension. Their data suggests that such forces increase over the course of extension, thus we use the latter of the two to compare our results at 0[ms] (Figure 3), which is where we assume takeoff to occur and peak leg forces to be generated. Differences such as their tethered preparation, their direct stimulation of the Giant Fiber neuron, and the dependence of their results upon leg angles could account for the discrepancy between the two measures.

In our approach, to estimate the contribution made by the legs, we measure leg-joint kinematics and construct

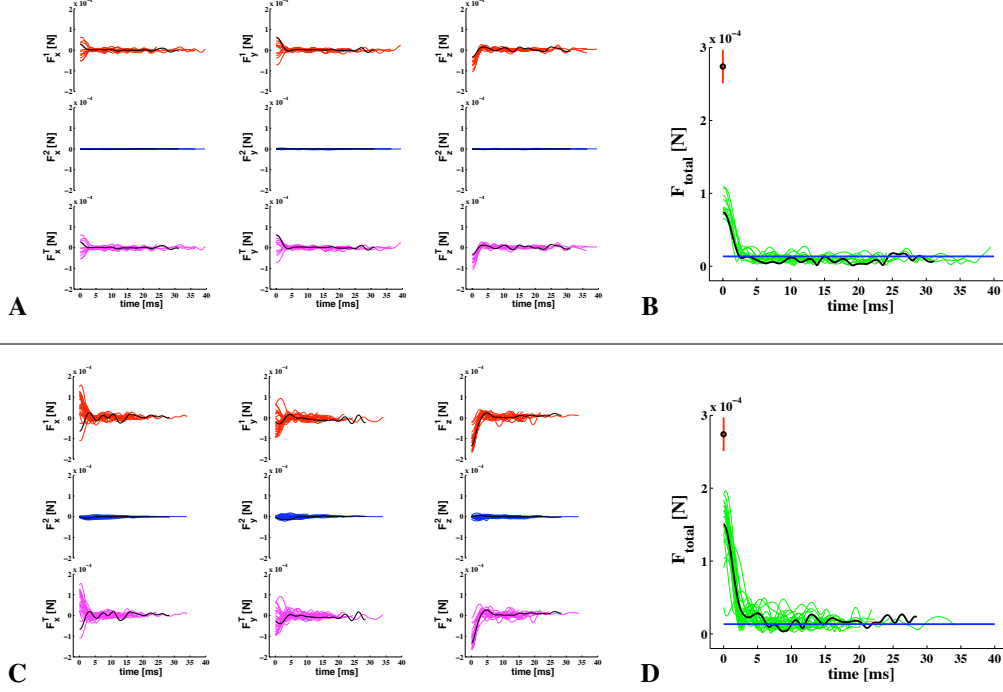


Fig. 3. Reaction forces during voluntary (A,B) and escape (C,D) take-offs. The black traces correspond to individual flies (one for escape data, another for voluntary) selected to represent the overall dynamic behavior. For the force data (A and C), the top traces represent the  $x$ - $y$ - $z$  components of the first term on the right-hand side of (1), while the middle traces correspond to the second term. The bottom traces show the total force, and its magnitude is depicted in B and D. The solid, horizontal trace, and the datum at (0 [ms], 274 [μN]) in B and D correspond to comparable results reported in literature (see text); meanwhile, the horizontal trace ( $t$ , 20.1 [μN]) represents the average force produced by the wings during forward flight [13] (comparable to both sets of data).

a model for simulation in which we can replay the measured values and calculate forces [4]. While in many cases it is desirable to reduce some complexity by ignoring a subset of DOF in the legs, for instance, when trying to build a mechanical device [15], we include in our model the six rotational DOF shown in Figure 4 given our interest in a comprehensive analysis. Next, to determine the forces and torques generated by the actuated joints during leg extension we can apply d'Alembert's principle to the kinematic data ( $\Theta$ ):

$$\tau_l = M(\Theta)\ddot{\Theta} + C(\Theta, \dot{\Theta})\dot{\Theta} + N(\Theta, \dot{\Theta}). \quad (2)$$

A caveat in this approach is that without a physical measurement, we are only estimating the apparent forces exerted by the fly (i.e., the ones generating the motion). In addition, our model represents leg segments as thin rods placing their respective center of mass at halfway of their total lengths. While this yields a rough approximation it can be refined to include realistic leg-segment inertias. Given that this part of our analysis is currently intended to establish a set of initial conditions for each of the flies' responses, the reconstruction of forces using

eq. (2) suffices.

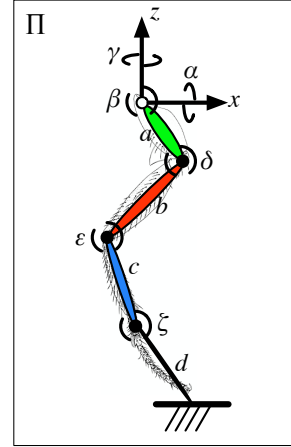


Fig. 4. Kinematic model of a single leg on the left side of the body [front-view]. In this case, the coordinate frame  $O'$  has been rotated counter-clockwise by  $\alpha$  degrees to the orientation indicated by the dashed arrows. In our representation, all leg segments always lie on a plane ( $\Pi$ ); the intended perspective of the image is  $\beta = \gamma = 0$ . Note that, the subscript  $l$  has been omitted in the figure for clarity.

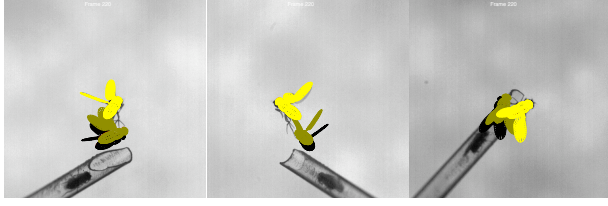


Fig. 5. Performance of the fly tracking algorithm on the three camera views for a particular image frame. Tracking results from few previous frames are superimposed for clarity.

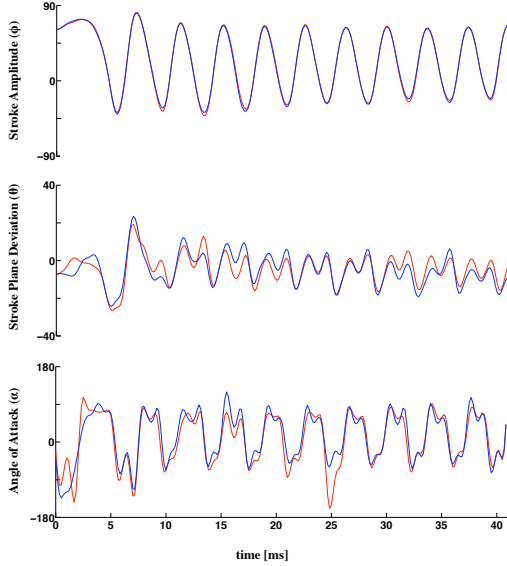


Fig. 6. Wing kinematics revealed by visual tracking algorithm used to calculate aerodynamic forces.

2) *Wing forces*: Constructing a dynamic model that captures the maneuvers employed by the fly in response to the leg action is the key to understanding the operation of its flight control mechanisms during takeoff. This feat entails the calculation of wing forces, which in a similar manner to the quantification of leg forces, can be estimated from extracted kinematic data of wing motion.

A visual tracking algorithm [2] allows extracting the necessary kinematic data (Figure 5 and 6), then, we make use of the aerodynamic model of flapping flight to determine lift and drag forces:

$$\begin{aligned} dF_{tr,L} &= \frac{1}{2} \rho C_{tr,L}(\alpha_w(t)) U^2(r,t) c(r) \\ dF_{tr,D} &= \frac{1}{2} \rho C_{tr,D}(\alpha_w(t)) U^2(r,t) c(r) dr \\ dF_{rot,L} &= \frac{1}{2} \rho C_{rot,L} \dot{\alpha}_w(t) U(r,t) c^2(r) dr, \end{aligned} \quad (3)$$

### III. CONCLUSIONS AND FUTURE WORK

The framework described in the paper aims at revealing the flight control mechanisms used by the fly during

visually-elicited takeoffs. The observed phenomenon of initial unsteadiness in these evasive responses, along with the quick recovery and settling to steady trajectories, represents an ideal case study for insect flight control.

An important aspect that is currently being incorporated into this framework is the control of directionality during takeoff. In [10] the authors have described a series of pre-jump motions that determine the direction of takeoff. As expected from our interpretation of the takeoff dynamics, the pre-jump postural adjustments seem to modify leg extension in order for the jump to propel the insect in a particular trajectory (away from the stimulus). These movements, however, may be largely responsible for the unsteadiness observed in visually-elicited takeoffs.

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