The aerodynamics of flight maneuvers in fruit flies

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Flying animals such as birds, bats and insects are extremely maneuverable, partly because their flapping wing flight platform is inherently unstable. Thus, in order to perform a rapid maneuver, the flapping wings need to produce only small amount of aerodynamic torque. We studied the maneuver dynamics of fruit flies using high-speed videography of freely flying flies and by using a physical aerodynamic model of a fruit fly[1,2]. Similar to many other insects and small birds, fruit flies flap their wings back and forth at a high wingbeat frequency (200 Hz). Throughout the wingbeat, the wings operate at very high angles of attack (~45°, Fig 1), which leads to the production of a Leading Edge Vortex (LEV) during each wing stroke. The LEV significantly boosts the aerodynamic lift required for weight support (Fig 1).

We studied two types of flight maneuvers in fruit flies, the body saccade and the evasive maneuver[1,2]. The body saccade (Fig 2A) is the sharp turn that flies produce at regular intervals during normal steady flight, and it is regarded as one of the most performed maneuvers found in nature[2]. The evasive turn (Fig 2B) is the very fast maneuver that is critical for survival because it is used to avoid collision and capture by predators[1].

We found that fruit flies control flight maneuvers very similar to helicopters. A fly primarily modulates the wingbeat-average aerodynamic force magnitude, of which the orientation remains roughly constant relative to the body (Fig 1).

Fig 1. The wing kinematics depicted as lolly-pops and aerodynamic g-force vectors throughout the wingbeat of a hovering fruit fly. Adapted from Muijres et al (2014).
The direction of the aerodynamic force is controlled by body rotations around the three body axes, the roll, pitch and yaw axis (Fig 3). As a result, maneuvers in flies consist of a banked turn whereby flies bank to rotate the wingbeat average lift force in the desired direction of the turn and then rotate back again to continue straight flight (Fig 2A,B).

Although both saccadic and evasive maneuver consist of banked turns, the underlying control dynamics that allows a fly to regulate turn angle (i.e. how far the fly turns) is very different. During the initial phase of the body saccade, a fly rotates its body around a very stereotypic bank axis, which consists of roughly 65% body roll and 35% pitch up (Fig 2C). To regulate the turn angle of the saccade, a fly adjusts the amount of body rotation, whereby a larger banking rotation leads to a larger turn angle. The turn angle of evasive maneuvers, on the other hand, is not regulated by adjusting amount of rotation but by varying the ratio between the roll and pitch up components of the bank (Fig 2D). This roll-pitch ratio directly depends on the relative position of the danger that the fly is evading from, such that when an object approached the fly from the front the fly produces a pure pitch-up maneuver, and when the danger comes from the rear the fly produces pure roll during the banking maneuver (Fig 2D). The difference in control dynamics between the two maneuver types can be explained by the requirements of both maneuvers.

For the saccadic turn, the fly needs to perform a turn as controlled as possible, and so a highly stereotypic maneuver is preferred, i.e. always rotating around the same axis. For the evasive maneuver, the fly needs to escape as fast as possible and so the maneuver is performed at maximum banking rate. Therefore, controlling the turn through banking rate is not feasible, and so varying the direction of the banking axis is used instead.

By data-mining all studied maneuvers, we extracted the wingbeat kinematics changes responsible for controlling aerodynamic force magnitude and torque production about the roll, pitch and yaw axes. By replaying these kinematics on a dynamically-scaled robotic model of a fruit fly, we then modelled the underlying aerodynamic forces on the wings (Fig 3).
We found that fruit flies control aerodynamic force magnitude primarily by adjusting wingbeat amplitude and flap frequency (Fig 3A). Pitch torque is modulated by adjusting the position of stroke reversal at the end of the upstroke, which shifts the wingbeat-average force forwards and backwards with respect to the center of mass (Fig 3B). Roll torque is produced by moving one wing further up at the end of the downstroke. During the start of the consecutive upstroke, that wing produces a stronger downward plunge, resulting in a larger upwards directed drag force. The asymmetry in upward force between both wings results in a roll moment (Fig 3C). Yaw is produced by operating one wing at a higher angle of attack during the downstroke, but at a smaller angle of attack during the upstroke. This results in an asymmetry in drag force production between the two wings causing a net yaw torque throughout the wingbeat (Fig 3D).

Because the fly controls pitch and roll torque at the two opposite parts of the wingbeat, pitch and roll torque regulation is both spatially and temporally separated. This might simplify the control of relative pitch and roll torque during the fast evasive maneuvers. Also, the changes in wingbeat kinematics responsible for the studied flight maneuvers are strikingly small. This might contribute to the flies’ ability to perform the very fast maneuvers that we measured, but it also means that the biological control actuators of the flight motor system need to be both very fast and precise to remain in control throughout not only the fast maneuver but even during inherently unstable straight flight.

**Fig 3.** The wing kinematics and aerodynamic forces throughout the wingbeat of fruit flies that (A) produce an increased lift force (in green, the grey data is the hovering kinematics from Fig. 1), (B) pitch up and down torque (in light blue and orange, respectively), (C) roll torque, and (D) yaw torque. For clarity, the downstroke and upstroke kinematics are separated (the crosses depict the wing hinge position).

**References**
