The Initiation and Control of Rapid Flight Maneuvers in Fruit Flies[1]

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SYNOPSIS. Fruit flies alter flight direction by generating rapid, stereotyped turns, called saccades. The successful implementation of these quick turns requires a well-tuned orchestration of neural circuits, musculo-skeletal mechanics, and aerodynamic forces. The changes in wing motion required to accomplish a saccade are quite subtle, as dictated by the inertial dynamics of the fly's body. A fly first generates torque to begin accelerating in the intended direction, but then must quickly create counter-torque to decelerate. Several lines of evidence suggest that the initial turn is initiated by visual expansion, whereas the subsequent counter-turn is triggered by the gyroscopic halteres. This integrated analysis indicates how the functional organization of neural circuits controlling behavior is rigidly constrained by the physical interaction between an animal and the external world.

INTRODUCTION

Insects were the first animals to evolve active flight, and remain unsurpassed in many features of aerodynamic performance (Dudley, 2000). In recent years, studies using a variety of methods including physical modeling, flow visualization, and computational fluid mechanics have converged to provide a more detailed understanding of flapping flight aerodynamics (Ellington *et al.*, 1996; Dickinson *et al.*, 1999*b*; Srygley and Thomas, 2002; Sane, 2003). Although critical issues remain, the basic means by which insects generate enough lift to stay aloft have been resolved and new research can more easily focus on the challenging question of how insects actively manipulate aerodynamic forces to steer and maneuver.

When considering the control of complex aerial behaviors, it is impossible to disentangle the aerodynamics of flapping from the mechanics of the wing hinge, the physiology of the flight muscles, or the properties of sensory-motor circuits in the brain. Thus, an integrative approach that addresses the functional interactions among these various components is essential for identifying the organizational principles of the flight control system. In this review, I will describe a single stereotyped flight maneuver of the fruit fly, *Drosophila melanogaster*, at several levels of analysis— from the sensory signals that trigger the behavior to the aerodynamic forces generated by the wings. The results show how the rules governing the physical interaction of an animal with the external world strongly influence the evolution of the neural circuits that control locomotion.

THE VISUAL CONTROL OF BODY SACCADES

When searching for food, fruit flies explore their landscape using a series of straight flight paths interspersed with rapid turns termed *saccades* (Fig. 1A).

These rapid turns were first rigorously characterized by Collet and Land in hoverflies (Collett and Land, 1975), but are exhibited by many dipteran species. During each saccade, a fruit fly changes heading by approximately 90° in 50 msec, completing the maneuver in about 10 wing strokes (Tammero and Dickinson, 2002*b*). When flying within a circular arena in the laboratory, the saccade rate is so regular that one is tempted to propose that each turn is triggered by an internal clock within the animal's brain. However, experiments suggest that each saccade is initiated by a specific sensory stimulus that the fly encounters as it flies through the air. By carefully tracking the flies within an arena lined with a printed visual pattern, it is possible to crudely reconstruct what the animal sees just prior to each saccade (Tammero and Dickinson, 2002*b*). Such an analysis suggests that flies turn away from visual expansion as they near obstacles. This behavior appears to represent a binary decision in that a fly either turns to the left or right, but does not adjust the magnitude of the turn depending on the strength of the visual stimulus. This feature of the behavior is most clearly seen when a fly flies directly through the center of the arena toward the opposite wall. Under these conditions the fly does not, as one might expect, exhibit a 180° turn, but rather makes the "choice" to turn 90° to either the left or right with equal probability (Fig. 1B, C). However, although the choice appears binary there is nevertheless enormous variance in the magnitude of the turn. Given that the neurons controlling this rapid behavior have only time enough to fire a few action potentials, the variability might arise from internal noise within flight control circuitry. However, it is also possible that the variance in saccade angle does represent an active modulation of motor output in response to features of the sensory input that have yet to be identified.

There are, however, several uncertainties in reconstructing the visual stimuli that trigger saccades based on free flight data. For example, the angular position of the body and head are not known and must be inferred from the animal's flight path. A more precise map of the visual reflexes may be reconstructed by
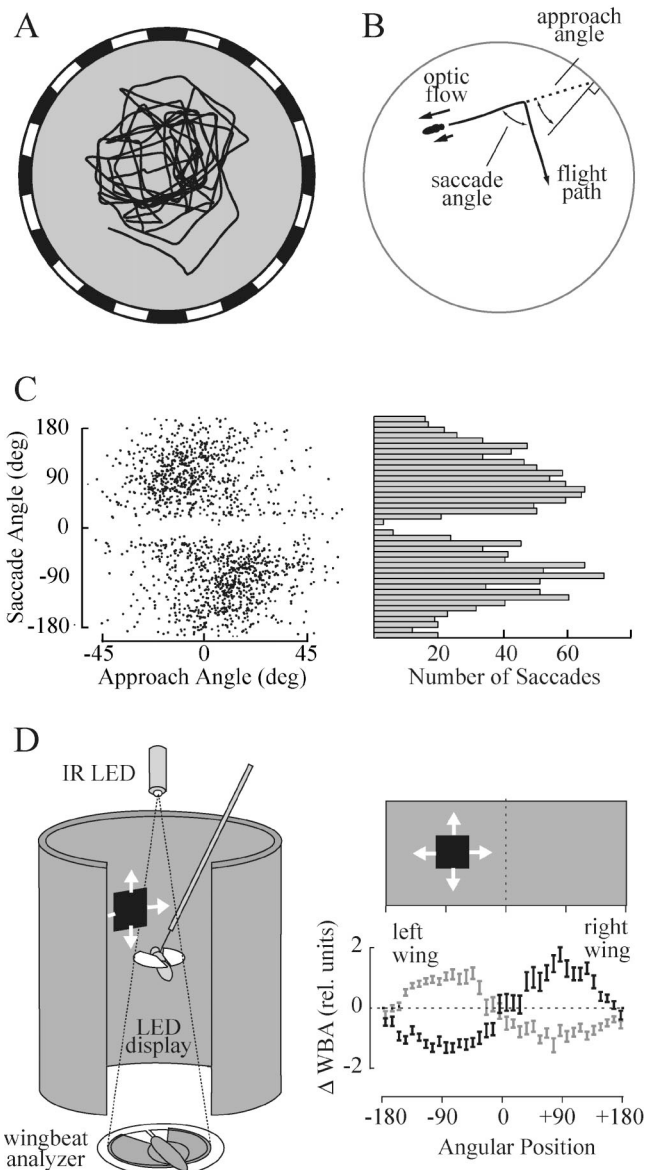
FIG. 1. Saccades are sharp, right angles turn elicited by visual expansion. (A) Flight trajectory of fruit fly seen from above. (B) Definition of saccade angle and approach angle. (C) Relationship between approach angle and saccade angle. Histogram of saccade amplitude shows that flies turn either left or right. (D) Experiments in tethered flight arena confirm the role of visual expansion in saccade initiation. See text for details. Modified from Tammero and Dickinson (2002a, b).

performing experiment on tethered animals flying within an electronic arena (Fig. 1D). The flight arena consists of an optical wingbeat analyzer that tracks the amplitude and frequency of the two wings and a cylindrical electronic visual display that presents moving visual patterns to the fly (Götz, 1987; Lehmann and Dickinson, 1997). The flight arena works in either *open-loop* configuration, in which one measures the fly's behavioral response to a set of visual stimuli, or in *closed-loop* configuration, in which the fly itself can control the visual display by altering its pattern of

wing motion—a simple form of "virtual reality." A convenient closed-loop experiment is the so-called fixation paradigm, in which a fly is permitted to control the azimuthal velocity of a narrow stripe or square by adjusting the relative stroke amplitude of its wings (Götz, 1987). Under such conditions, a fly will actively steer towards the object, maintaining it in the front field of view. To study the expansion response, the fly is allowed to fixate a small square in the presence of an oscillating bias (the equivalent of an electronic "cross wind") which makes the task more difficult (Tammero and Dickinson, 2002a). At random intervals the square is programmed to rapidly expand, thereby eliciting flight control reflexes. If the square expands to the animal's left, the left wingstroke amplitude transiently increases and the right wingstroke decreases. The opposite occurs if the expansion takes place on the animal's right. As discussed later, such changes in wing motion would have the aerodynamic effect of turning the animal away from the expanding stimulus. The results are consistent with free flight studies, and suggest that the saccade trigger circuitry might consist of a simple bilateral pair of expansion-detector circuits within the visual system. The tethered flight experiments also reveal that flies rapidly extend their legs and elevate wing beat frequency in response to frontal expansion—a reflex that is known as the landing response (Borst, 1990). Thus, the net behavioral response to visual expansion can be explained by three expansion detectors (one for the landing response, two for bilateral collision avoidance responses), each driving independent motor pathways. However, the terms "collision avoidance" and "landing response," though convenient, ascribe specific functions to these behaviors that have yet to be definitively demonstrated. It is possible, for example, that the kinematic changes during a landing response would actually cause an animal to pitch up and hover as it approaches an object. This ambiguity exemplifies the difficulty of predicting free flight behaviors from tethered flight responses.

ORGANIZATION OF MUSCULO-SKELETAL SYSTEM

A combination of free flight and tethered flight experiments indicate that flies reflexively turn away from expanding visual patterns through a rapid and coordinated change in wing motion. How does the fly's nervous system enact these changes in motor output? The flight musculature of flies is segregated into two anatomically-, physiologically-, and functionally-distinct groups (Fig. 2A) (Heide, 1983; Dickinson and Tu, 1997a). Most of the thoracic volume is filled with large indirect flight muscles (IFMs) that generate the elevated mechanical power required for flight. Despite their critical role in driving wing motion, these muscles do not insert directly at the base of the wing. Rather, antagonistic sets of muscles run front-to-back (dorso-longitudinal muscles, DLMs) and top-to-bottom (dorso-ventral muscles, DVMs) within the thorax. An elaborate mechanical coupling system within the exoskeleton of the thorax transforms the small strains

A

IFMs

upstroke muscles   downstroke muscles   Steering Muscles

B

upstroke
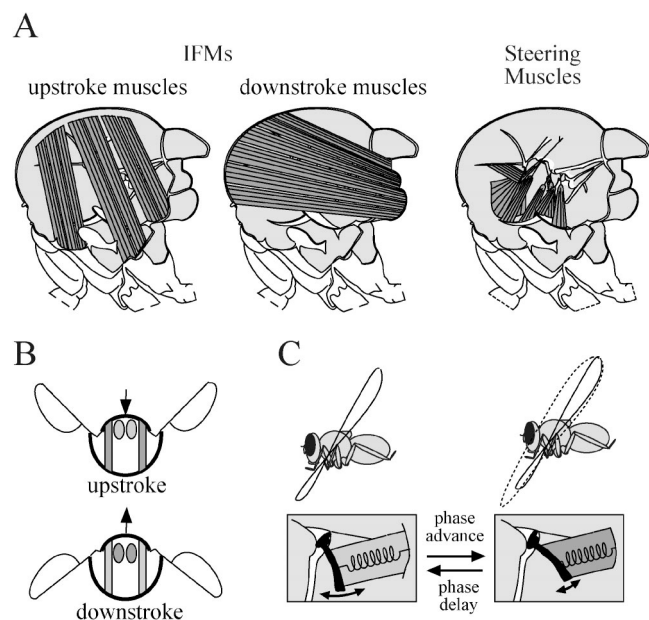
downstroke

C

phase advance

phase delay

FIG. 2. Organization and function of flight muscles. (A) Powerful indirect flight muscles (IFMs) are arranged in two antagonistic groups. Tiny steering muscles insert directly at the base of the wing hinge. (B) The IFMs drive the gross pattern of wing motion. (C) Changes in recruitment and firing phase of steering muscles produce subtle changes in the wingstroke. Modified from (Dickinson and Tu, 1997*b*).

generated by the IFMs into the large sweeping motion of the wings (Wisser and Nachtigall, 1984; Miyan and Ewing, 1985; Wisser, 1988). In addition to this *indirect* pattern of insertion, the IFMs are also *asynchronous,* such that individual contractions are not controlled by spikes in pre-synaptic motor neurons in the conventional one-for-one fashion (Boettiger and Furshpan, 1952; Dickinson *et al.*, 1998). Rather, actin-myosin cycling is activated mechanically by stretch, and de-activated by shortening (Josephson *et al.*, 2000). Because the two sets of antagonistic IFMs are oriented orthogonally within the thorax, contractions in one set activate the other after a short delay, and the entire system functions as a mechanical resonator (Fig. 2B) (Jewell and Ruegg, 1966). The advantage of this arrangement is that asynchronous muscles can generate sufficient power at high frequency without an extensive sacroplasmic reticulum (SR), which is required in traditional twitch muscle so that it deactivates during the lengthening stage of a locomotor cycle. Reducing the requirement for SR frees the internal volume for more contractile fibrils and mitochondria (Josephson and Young, 1987), which explains the power-generating ability of asynchronous muscle at the high frequencies required for flight in small insects. This impressive system has evolved multiple times in insects, and is associated with the adaptive radiation of small body size (Dudley, 2000).

The very specializations that enable the IFMs to generate mechanical power make them ill-suited for the rapid control of wing motion during saccades. This task falls upon a dozen or so small conventional *synchronous* muscles that insert directly on scleritized elements within the exoskeleton at the base of the wing (Heide, 1983; Wisser and Nachtigall, 1984). Acting as a transmission system, these steering muscles alter the mechanics of the wing hinge thereby regulating how the mechanical energy of the IFMs is transformed into wing motion. Because of their essential role in regulating wing motion, these muscles represent a critical bottleneck in the flight control system.

With few exceptions, each steering muscle is innervated by a single motor neuron (Trimarchi and Schneiderman, 1994), which due to the high wing beat frequency, can fire no more than one spike within each stroke. Thus, the fly's nervous system can typically only control two parameters: whether a particular muscle fires within a given wing stroke and the phase at which it does. Electrophysiological experiments in *Drosophila* have shown that three of the largest steering muscles (Mb1, Mb2, and MI1) can account for many of the changes in wing motion during saccades and other maneuvers (Heide and Götz, 1996; Lehmann and Götz, 1996). Evidence suggests that large changes in stroke amplitude from one stroke to the next are brought about by recruitment of normally quiescent muscles Mb2 and MI1, whereas changes in the firing phase of the tonically active Mb1 are responsible for more subtle alterations (Tu and Dickinson, 1996; Balint and Dickinson, 2001). The phase-controlled role of Mb1 is of particular interest because, as will be discussed later, the changes in wing motion during saccades are quite small.

How can tiny changes in firing phase alter the mechanical properties of a steering muscle? Recent comparative work in many animals suggests that, in addition to their role as force generating actuators, muscles can perform many different mechanical tasks within an animal, including roles as struts, brakes, and springs (Dickinson *et al.*, 2000). Biophysical studies show that when cyclically loaded, the dynamic stiffness of fly steering muscles varies with activation phase (Tu and Dickinson, 1994). Thus, the fly brain can use the steering muscles as variable-stiffness springs that may be controlled on a cycle-by-cycle basis by adjusting firing phase (Fig. 2C).

MECHANOSENSORY FEEDBACK

If firing phase determines the biomechanical properties of the steering muscles, and as a consequence the precise motion of the wings, what signals tell the muscles when to fire? Experiments in which sensory nerves were systematically ablated indicate that the firing phase of steering motor neurons is driven, not by a central pattern generator, but rather by mechanosensory afferents on the wing and haltere (Heide, 1983). The wing is equipped with arrays of *campaniform sensilla*, strain-sensitive structures imbedded within the exoskeleton (Cole and Palka, 1982; Gnatzy *et al.*, 1987). In blowflies, a subset of these sensors make strong monosynaptic connections with the motor neu-

rons of steering muscles (Fayyazuddin and Dickinson, 1996). Stroke-by-stroke input from wing sensors is capable of entraining steering motor neurons, thus ensuring that muscles fire at particular phases within the cycle (Fayyazuddin and Dickinson, 1999).

Halteres are the tiny club-shaped hindwings characteristic of all flies. During flight, the halteres beat in precise anti-phase with the forewings, thereby activating several hundred specialized mechanosensory cells at the base of the structures. The sensory cells are organized into five external fields of campaniform sensilla and one internal chordotonal organ (Pringle, 1948). Most of the fields encode the back and forth motion of the haltere in stable flight, and thus may act as their homologues on the wing to provide important timing signals to lock the steering muscles into particular phases of the stroke cycle. However, one of the campaniform fields (dorsal field 2, dF2) appears unique in that it is not sensitive to the back and forth beating of the haltere, but instead encodes the deflection of the haltere perpendicular to its stroke plane. During flight, such deflections are caused by Coriolis forces (Pringle, 1948; Nalbach, 1993), which act on the rapidly beating halteres whenever the fly's body rotates. The Coriolis-sensitive cells of dF2 make mixed electrical/chemical synapses with the motor neurons of steering muscles (Fayyazuddin and Dickinson, 1996; Trimarchi and Murphey, 1997), which are strong enough to temporarily override the phasic input from the wing afferents (Fayyazuddin and Dickinson, 1999), thereby shifting the timing of muscle activation in each stroke (Fig. 3B). Such modulation in steering muscle activity presumably causes alterations in wing motion and aerodynamic forces.

The critical role of the haltere in flight stability was first identified in 1714 by William Derham, who showed that a fly could not remain airborne if its tiny halteres were surgically removed (Derham, 1714). Recent experiments on animals tethered within rotating flight simulators indicate that animals exhibit robust compensatory changes in wing amplitude and frequency to imposed mechanical rotation (Fig. 3C) (Nalbach and Hengstenberg, 1994; Dickinson, 1999). The sign of the reflexes are such that they would act to counter any imposed perturbations, bringing the animal back to a stable orientation.

The haltere-motor circuits that counteract imposed rotation are so rapid and robust that it raises the question of how such reflexes are over-ridden during voluntary maneuvers such as saccades. One possibility is that the nervous system can adjust the gain of haltere reflexes to inhibit them during voluntary behaviors. In the blowfly *Calliphora*, descending visual interneurons activate tiny steering muscles of the haltere. By altering the kinematics of haltere motion, these steering muscles might either increase or decrease the sensitivity of the Coriolis-sensitive sensilla (Chan *et al.*, 1998). Alternatively, if this descending input to haltere steering muscles produces changes in the haltere stroke plane that mimic those produced by rotation of the
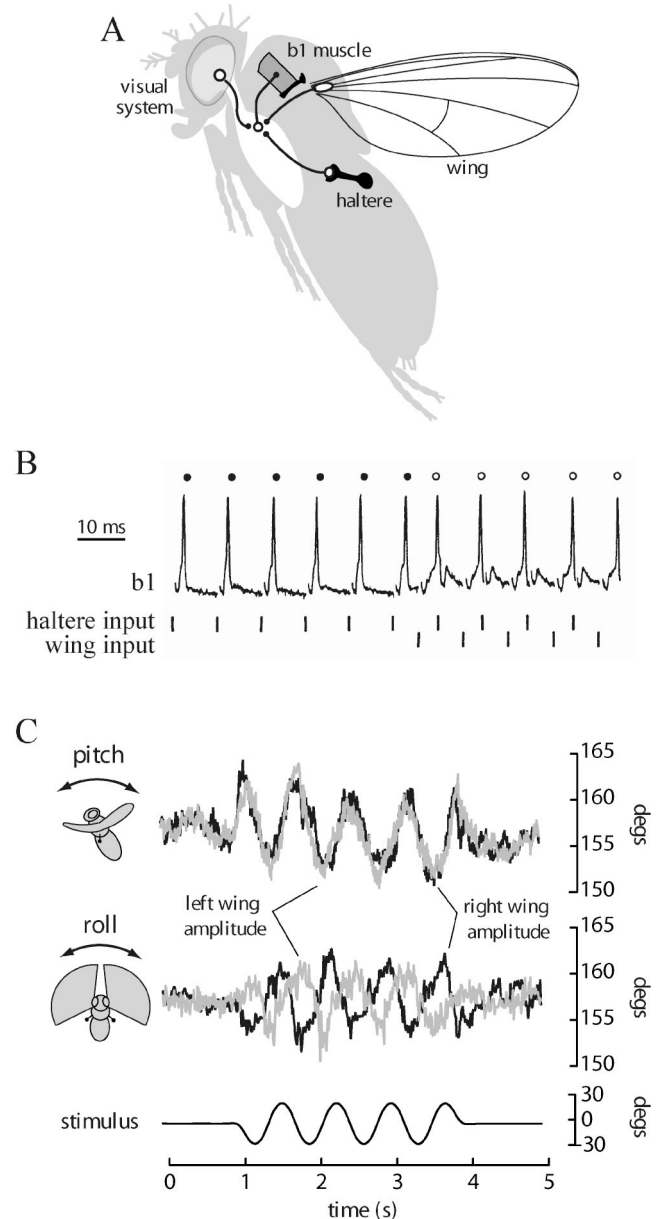

FIG. 3. Haltere-mediated flight reflexes. (A) Simplified diagram of flight control circuits. Descending visual input is thought to converge with mechanosensory input from wing and haltere on motor neurons of steering muscles such as b1. (B) In *Calliphora*, input from wing mechanoreceptors can repetitively drive spiking in the b1 motor neuron. When active, haltere input can over-ride the wing input, advancing the phase of the motor neuron. Modified from (Fayyazuddin and Dickinson, 1999). (C) Mechanical rotation, encoded in part by the halteres, elicits compensatory changes in stroke amplitude. Modified from (Dickinson, 1997).

body, then the system might function to initiate voluntary maneuvers by generating "virtual" flight perturbations. This would be analogous to steering an aircraft by fooling an autopilot into responding to a nonexisting course deviation. A third possibility is that the haltere-mediated reflexes are always operational, but that descending commands perturb the system just long enough to result in a change in flight path.

One of the most critical tasks of flight control circuitry is to integrate local mechanosensory feedback from the wings and halteres with descending commands from the visual system, such as those that trigger saccades. This fusion of sensory feedback is complicated by the fact that the visual and olfactory systems transduce and process sensory information on a slow time scale compared to the mechanoreceptors on the wing and haltere (Heide, 1983). Because the raw output from the visual system is not phase-locked with wing motion, it is inappropriate as direct input to steering motor neurons. Somehow the nervous system must combine descending commands with phasic input from thoracic mechanoreceptors so that the visual circuits activate steering at biomechanically-appropriate phases of the stroke cycle. How flight circuits accomplish this critical splicing of descending commands with phasic feedback is not well understood. Descending commands, such as the expansion signals that trigger saccades, are conveyed by a set of descending interneurons that project to flight circuits in the thorax. Anatomical evidence in blowflies suggests that descending visual interneurons make direct connections with steering motor neurons (Strausfeld and Gronenberg, 1990). Thus, one possibility is that the splicing or chopping of descending information with thoracic feedback takes place via synaptic interactions directly on the dendrites of steering motor neurons. However, mechanoreceptors on the wing and halteres possess collateral projections that ascend to the subesophageal ganglion, where they could potentially converge on visual circuits upstream of the descending interneurons (Chan and Dickinson, 1996). Thus, it is also possible that the critical fusion takes place in the brain so that the descending commands are already phase-locked to the stroke cycle.

Aerodynamics of Saccades

Studies on both real and robotic insects over the past 12 years have revealed much about the aerodynamics of insect flight (Sane, 2003). The unusual aerodynamics of flies and many other insects results from the peculiar reciprocating motion of their wings. Rather than moving forward while flapping their wings up and down like a bird, flies hover while beating their wings back and forth. At the end of the downstroke, the wing pitches up and flips over, so that it maintains a positive angle of attack during the upstroke, with the leading edge forward but the ventral surface facing up. A reverse rotation at the end of the upstroke readies the wing for the downstroke. Depending on the precise form of this back-and-forth pattern, the wings can generate forces by the variety of different mechanisms.

The primary means by which a fly wing creates aerodynamic force is *dynamic stall*. Due to its large angle of attack, the wing separates flow creating a prominent leading edge vortex (LEV) (Dickinson and Gotz, 1993; Ellington *et al*., 1996). Unlike similar structures created by a 2-dimensional translating wing (Dickinson and Gotz, 1993), a revolving wing (*i.e.*, one that sweeps around a fixed base) creates a stable LEV that remains attached throughout the stroke (Birch and Dickinson, 2001; Usherwood and Ellington, 2002; Birch and Dickinson, 2003). The term "dynamic stall" is therefore misleading, because the flow, although separated, is time-invariant with respect to the wing once the LEV has formed. The constant circulation that results from the stable LEV is responsible for steady force production of sufficient magnitude to sustain flight. In addition to dynamic stall, flapping wings can generate force by additional means including *rotational force, wake capture,* and *added mass* (Dickinson *et al*., 1999*a*; Sane, 2003). By changing the shape and inclination of the wing stroke and the speed and timing of wing rotation, an individual insect can dramatically alter the relative contributions of the various aerodynamic mechanisms from one stroke to the next (Srygley and Thomas, 2002).

Equipped with a better understanding of the basic relationships between wing motion and force production, it is now possible to study the aerodynamics of specific flight maneuvers such as saccades (Fry *et al*., 2003). When hovering, fruit flies move their wings back and forth in almost perfect mirror symmetry (Fig. 4A). The mean stroke plane is nearly horizontal, and the wings follow a "U-shaped" trajectory. The aerodynamic forces resulting from this pattern of wing motion were measured by playing the kinematics through a dynamically-scaled robotic insect (Dickinson *et al*., 1999*b*). The wings generate a large force peak near the middle of the upstroke and a smaller peak near the middle of the downstroke. Although the upstroke produces more lift due to a stronger vertical plunge, the horizontal force (thrust) generated during the upstroke and downstroke is nearly equal and opposite, consistent with the low forward velocity. By comparing measured forces with a multi-component quasi-steady model (Sane and Dickinson, 2002), it is possible to quantify the relative importance of different aerodynamic mechanisms. In the case of hovering, dynamic stall accounts for about 80% of the mean force produced and predicts the overall time course of measured forces.

Flies use remarkably minor alterations in wing motion to generate saccades. In addition, the forces measured relative to the animal's body axis change very little throughout the maneuver. The alterations of lift and thrust during the saccade result from the changing orientation of the body, just as a helicopter can increase thrust by pitching downward. Thus, understanding how the fly controls body orientation is central to the analysis of flight maneuvers. To rotate about its yaw axis, a fly must overcome its moment of inertia as well as frictional damping. The torque required to do so, T_ϕ, may be approximated as:

$$T_\phi = I_\phi \, d^2\phi/dt^2 + C_\phi d\phi/dt,$$

where I_ϕ and C_ϕ are the moment of inertia and frictional damping about the yaw axis, and ϕ is yaw position. Prior models of fly flight have assumed that
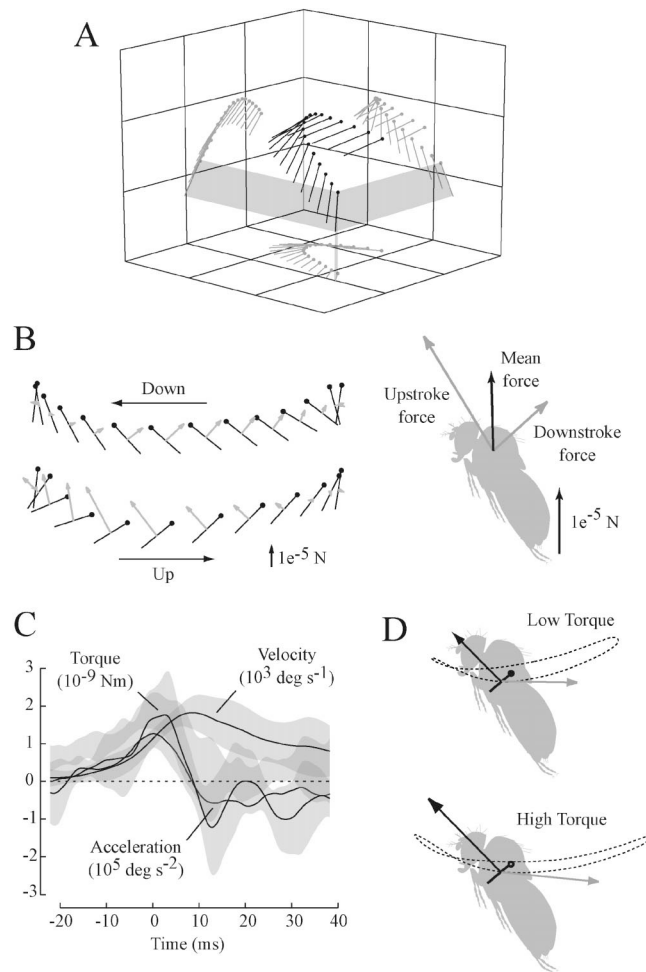
FIG. 4. Kinematics and dynamics of saccade. (A) Changes in body motion during saccade. (B) Wing motion and resultant forces during hovering. Mean flight force during hovering indicated on fly at right. (C) Torque, velocity, and acceleration about the yaw axis during saccade. (D) Wing patterns generating low and high yaw torque. Data modified from (Fry *et al.*, 2003).

viscosity dominates the dynamics of rotation so that an animal would instantly reach terminal angular velocity (Land and Collett, 1974; Reichardt and Poggio, 1976). However, the measured time course of T_ϕ, measured by playing the saccade kinematics on the robot, is similar to that of the fly's angular acceleration, not its angular velocity (Fig. 4C). This suggests that the dynamics of this small insect are dominated by body inertia and not friction. Estimates of I_ϕ and C_ϕ based on body morphology closely match those based independently on the free flight kinematics and forces. In both cases the predicted time constant (I_ϕ/C_ϕ) is between 0.5 to 1sec, or roughly 10 to 20 times the duration of a single saccade. Thus, a fly would never approach terminal angular velocity during a saccade. This dominance of inertia has important consequences for the generation of saccades and flight control in general. A fly cannot rely on air friction to stop its motion at the end of a turn. Instead, it must create

counter torque in the opposite direction to terminate a saccade.

Following a trigger from the visual system, how does a fly alter its wing motion to first initiate and then terminate a saccade? Two specific changes in wing motion correlate most strongly with measured yaw torque: a backward tilt of the stroke plane and an increase in stroke amplitude (Fig. 4D). The backward tilt of the stroke plane elevates flight force during the upstroke by increasing the aerodynamic angle of attack. An increase in stroke amplitude further augments force by elevating wing velocity. At the onset of a saccade, the outside wing undergoes these changes, thereby creating torque to rotate the body at the start of the turn. After about 20 ms the inside wing exhibits similar changes, thereby generating counter-torque to terminate the saccade. Although the changes in wing kinematics and moments are subtle, analysis of the resulting forces indicate that they are nevertheless sufficient to rotate the fly's body through the turn (Fry *et al.*, 2003),

If a visual expansion triggers the production of torque that starts the saccade, what is responsible for triggering the counter-torque that terminates the maneuver? Does the entire turn/counter-turn behavior represent a single pre-programmed reflex, or are the two phases of the behavior triggered by separate sensory signals? Several lines of evidence suggest that the halteres may play a crucial role in triggering the counter-turn. The fictive saccades of rigidly tethered animals are much longer than free flight saccades, whereas those of loosely tethered animals, free to rotate around their yaw axis, are intermediate (Mayer *et al.*, 1988). The most parsimonious explanation for this result is that sensory systems detect the rotation at the onset of each saccade and initiate a compensatory counter signal to terminate the turn. Because of the intrinsic dynamics of phototransduction and motion processing, the visual system is much less sensitive to rapid rotation than is the mechanosensory-based haltere system (Sherman and Dickinson, 2003). Thus, the halteres are the most likely source for the sensory signal that initiates the counter-turn to terminate each saccade. This notion is supported by the observation that the angular magnitude of free flight saccades are not substantially increased by reducing the contrast of a surrounding visual panorama (Tammero and Dickinson, 2002b).

CONCLUSIONS

A working hypothesis for the control and dynamics of rapid flight maneuvers begins to emerge from an analysis linking aerodynamics, biomechanics, and neurobiology (Fig. 5). As a fly explores its sensory landscape, specialized expansion-sensitive circuits in the visual system detect obstacles and initiate all-or-none body saccades. Descending interneurons carry a trigger signal to the thorax that activates the motor neurons of a small set of steering muscles. Because the changes in wing motion required to steer are so subtle,
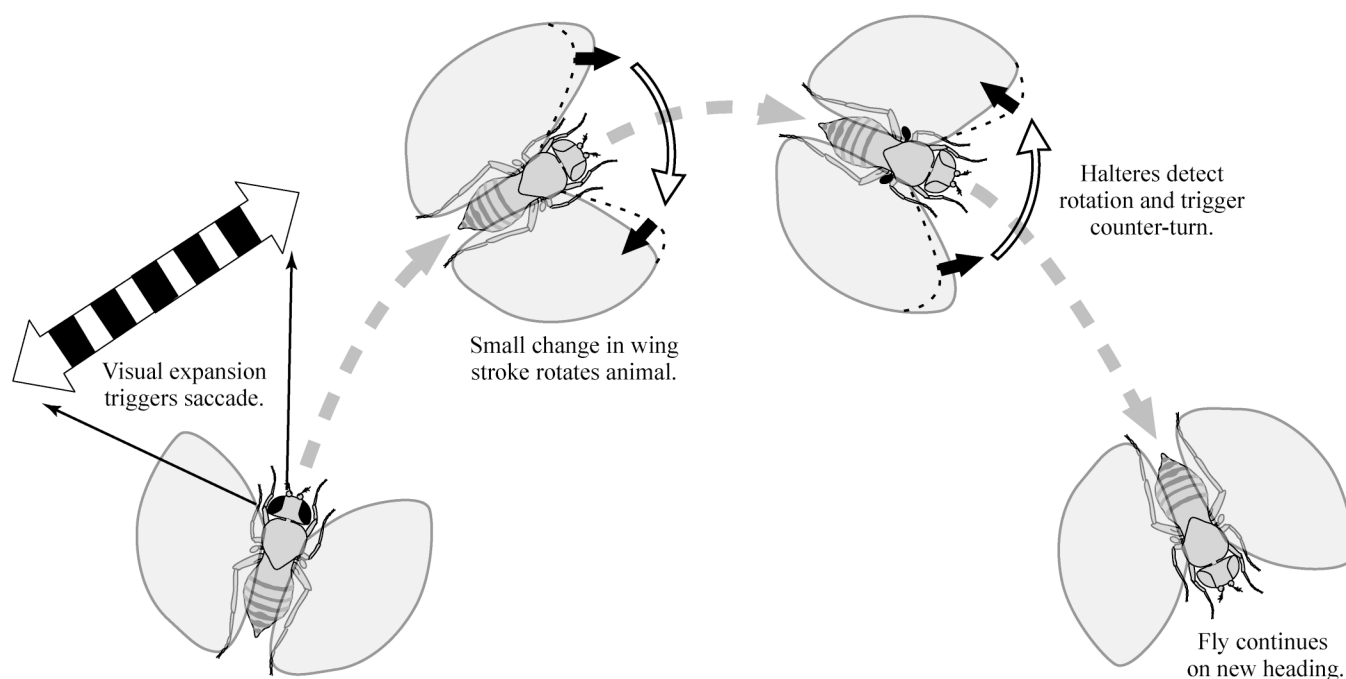
FIG. 5. Schematic model of saccade. See text for details.

they are probably brought about by small shifts in firing phase, which function to adjust the dynamic stiffness of muscles and alter the transmission mechanics of the wing hinge. The resulting changes in wing motion, though minor, are large enough to generate sufficient torque to turn the animal away from the looming obstacle. After only 4 or 5 wing strokes, the halteres detect this angular motion and trigger a compensatory counter-turn that decelerates the animal and terminates the saccades after a rotation of only 90°. Collectively, these results provide an important basis for future research on the control of insect flight, as well as insights for the design of biomimetic flying devices.

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