THE ACTIVE CONTROL OF WING ROTATION BY *DROSOPHILA*

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Summary

This paper investigates the temporal control of a fast wing rotation in flies, the *ventral flip*, which occurs during the transition from downstroke to upstroke. Tethered flying *Drosophila* actively modulate the timing of these rapid supinations during yaw responses evoked by an oscillating visual stimulus. The time difference between the two wings is controlled such that the wing on the outside of a fictive turn rotates in advance of its contralateral partner. This modulation of ventral-flip timing between the two wings is strongly coupled with changes in wing-stroke amplitude. Typically, an increase in the stroke amplitude of one wing is correlated with an advance in the timing of the ventral flip of the same wing. However, flies do display a limited ability to control these two behaviors independently, as shown by flight records in which the correlation between ventral-flip timing and stroke amplitude transiently reverses. The control of ventral-flip timing may be part of an unsteady aerodynamic mechanism that enables the fly to alter the magnitude and direction of flight forces during turning maneuvers.

Introduction

Whether cruising through an open field or circling a garbage can, flies impress us with their remarkable aerodynamic maneuverability. How is this sophisticated flight control achieved? Like all well-controlled locomotory systems, flies must rapidly integrate incoming sensory information and appropriately modify their motor output. The dominant sensory modality in flight control is undoubtedly the visual system, which has been the subject of extensive study (for reviews, see Heisenberg and Wolf, 1984; Strausfeld and Lee, 1991). Much less is known, however, of how the processed visual information modifies motor patterns to effect changes in the production of flight forces. Steering behavior has been most extensively studied in the vinegar fly *Drosophila* and the blowfly *Calliphora*. The presentation of optokinetic stimuli elicits changes in abdominal posture, leg position, wing-beat amplitude and head orientation (Nachtigall and Wilson,

1967; Götz *et al.* 1979; Hengstenberg *et al.* 1986; Zanker, 1988*a*, 1990*b*). Of these behaviors, bilateral differences in stroke amplitude are thought to be most important for the modulation of the bilateral forces necessary for the production of yaw forces (Götz, 1968, 1983; Götz *et al.* 1979; Nachtigall and Roth, 1983; Heisenberg and Wolf, 1984). However, application of the quasi-steady-state theory to measured changes in wing-beat kinematics in *Drosophila* results in predicted turning forces that are much smaller than those actually observed (Zanker, 1990*b*), suggesting that the control of flight maneuvers must reside in unsteady aerodynamic mechanisms and previously unrecognized kinematic changes of the wing stroke.

In addition to pure translation, insects actively rotate their wings during flight (Wooton, 1981; Ellington, 1984*a*; Ennos, 1989). In *Drosophila*, the most rapid rotation occurs during the transition from downstroke to upstroke. This rapid flip was termed the *quick rotation* by Zanker (1990*a*), who estimated that during this behavior the angular velocity of the wing exceeds 10^5 degrees s^{-1}. In order to distinguish this behavior from other rotations that occur during the wing beat, we will refer to this rapid supination as the *ventral flip,* because it occurs near the ventral-most position of the wing stroke. The ventral flip is present in other dipteran species besides *Drosophila* (Nachtigall, 1979; Ennos, 1989) and may be a ubiquitous feature of insect flight, particularly among species that utilize a horizontal stroke plane. In previous studies it was assumed that the flip occurred *synchronously* on the two wings and, thus, could not contribute to the production of yaw forces by the fly. In this paper, however, we report that the timing of the ventral flip is actively modulated during visually induced turning responses of tethered flies and could play an important role in course control.

The purpose of this paper is twofold: first, to describe the basic phenomenology of ventral flip modulation and, second, to examine its relationship with another well-established characteristic of the turning response, the modulation of wing-beat amplitude. From these observations we will propose a model by which the fly might employ the independent control of wing-beat amplitude and ventral-flip timing to produce a flexible system of flight control.

Materials and methods

Animals

All experiments employed laboratory stocks of the Berlin strain of *Drosophila melanogaster*. The data presented in the paper came from 1- to 5-day-old female flies, chosen because of their large size and behavioral robustness. Males do exhibit a modulation of the ventral flip behavior, but do not perform as rigorously as females in the flight arena. In preparation for an experiment, several dozen flies were anesthetized by low temperature. From these, we selected individuals that appeared healthy and undamaged under stereo optics. The animals were fixed to a tungsten rod tether by Glaskleber adhesive, which was polymerized by a 30s exposure to ultraviolet light. Flies were typically mounted to their tether in the evening, given a small tissue ball soaked with sugar water in a humid chamber, and tested the following morning. This rest period was to diminish any temporary adverse effects of the cold anesthesia or the ultraviolet light.

Experimental apparatus

The experimental method for measuring wing-beat kinematics in real time is indicated schematically in Fig. 1 and has previously been described in more detail (Götz, 1987*a*). Infrared diodes mounted above the fly cast shadows of the wings onto photodetectors positioned below. The crescent-shaped aperture above each photodetector traces out a section of the stroke envelope of the wings. The relative positions of the wings can be determined because the widths of the apertures increase monotonically from top to bottom. Thus, when the wings are moving through the ventral portion of the wing beat, their shadows block out a proportionally larger amount of light from the infrared photodiodes. However, the output of the photodiodes provides a somewhat distorted record of wing position because the stroke 'plane' is not perfectly flat and the transmittance signal is also dependent upon the angular orientation of the wing. Nevertheless, the magnitude of the peak shadow during each wing beat provides a real-time signal that is roughly proportional to stroke amplitude (Fig. 1B).

The raw signals generated by the wing-beat analyzer include a sharp transmittance spike near the time when the wings pass through their ventral-most position (Fig. 1B). These rapid, local transmittance maxima result from the quick supination of the wings during the ventral flip. As the wings rotate from dorsal side up to ventral side up, they pass through a position in which they are nearly parallel to the incident beam of light. The timing of these events was determined by analog peak detectors and transformed into
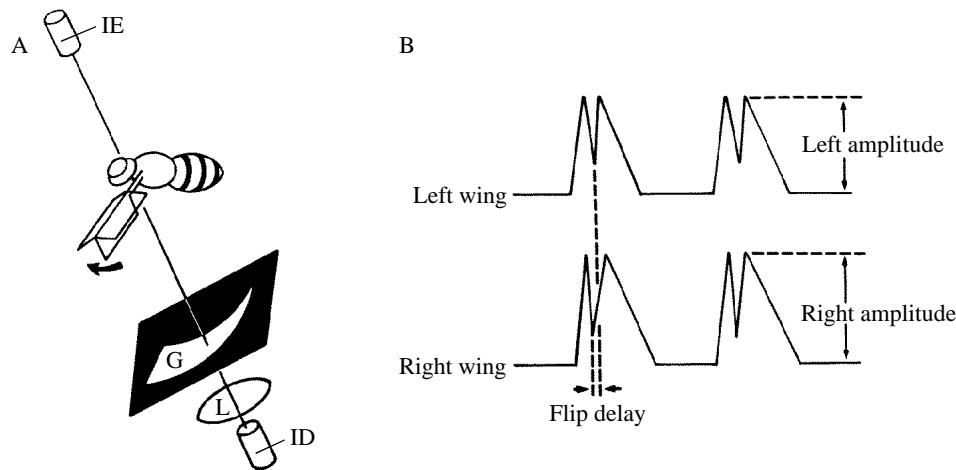

Fig. 1. The method used for determining wing-beat amplitude and ventral-flip timing. The method for measuring wing-beat kinematics in real time has previously been described in more detail (Götz, 1987*a*). (A) An infrared detector (ID) and lens (L) are used to track the movement of the shadow cast by the wing as it moves through light from an infrared emitter (IE) above the fly. The width of the grating (G) increases monotonically so that maximum occlusion takes place during the downstroke. (B) A sharp local transmittance peak is produced during the ventral flip when the wing becomes instantaneously aligned with the incident light. The waveforms generated by photodetectors for both wings are used to calculate relative wing-beat amplitude and ventral-flip delay.

digital pulses. These pulses were then processed on-line to construct a d.c. signal proportional to the time delay between the ventral flip on the two wings.

A simple visual pattern was projected through a circular painted-glass slide above the fly onto a surrounding cylinder (Götz, 1987a). The pattern consisted of a dark vertical stripe on a bright background. The position of the glass slide, and thus the stripe, was controlled by a servo motor and monitored using a co-axially mounted pancake potentiometer. In the open-loop configuration, the position of the servo motor was driven sinusoidally by a function generator at specified frequencies and amplitudes. In the closed-loop configuration (Heisenberg and Wolf, 1984; Götz, 1987a,b), the velocity of the servo motor was controlled by a d.c. signal representing the relative wing-beat amplitude, the ventral-flip delay or a linear combination of the two. Both the gain of the control signal and a bias were adjusted in each closed-loop experiment in order to stabilize the fly's response. The experiments were recorded on a seven-channel Racal tape recorder and subsequently digitized for analysis on a microcomputer. From the raw data, the following waveforms were constructed: relative wing-beat amplitude, relative ventral-flip timing and pattern position. The changes in wing-beat amplitude could be roughly calibrated to angular changes in the wing-beat envelope.

Results

Flies closely track the position of an oscillating vertical stripe with changes in ventral-flip timing as shown in Fig. 2. The sign of modulation is such that, as the stripe is located to the animal's left, the right wing tends to flip in advance, whereas the left wing leads when the stripe is located on the right. Thus, the wing on the outside of a fictive turn flips
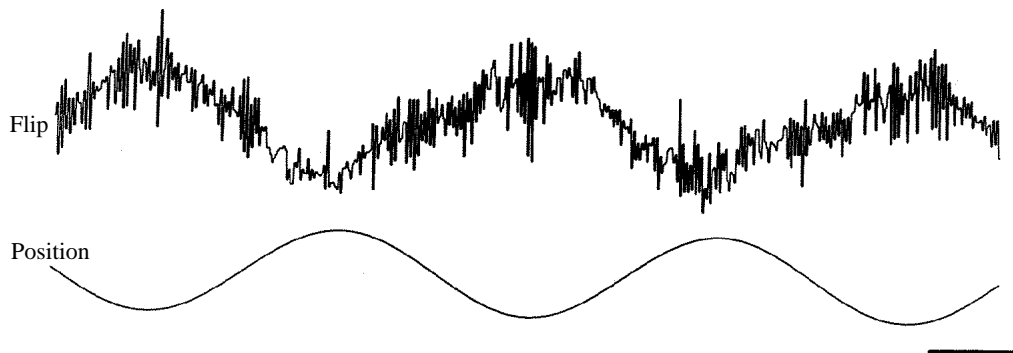

Fig. 2. Ventral-flip timing is modulated during visually induced maneuvers. A tethered fly was stimulated by 1Hz oscillation of the dark vertical stripe, eliciting an active modulation of ventral-flip timing. In this and all subsequent figures, an advance of the right wing and stripe movement to the fly's right are plotted upwards. As the vertical stripe moves to the fly's left, the right wing leads; when the stimulus moves to the right, the left wing flips in advance of the right wing. In this trace, the data are shown without filtration in order to show the rapidity with which the flip delay may change from one stroke to the next. Calibration bars: flip timing ±70 μs; stripe position ±90°; time 250ms.

in advance of the inside wing. The peak difference in timing between the supinations of the two wings elicited by a 180° oscillation of the dark stripe varied typically from 40 to 70 μs, corresponding to a phase difference of 3–5° with respect to one wing-beat cycle. Changes in the flip delay could be quite rapid, as indicated in Fig. 2, which shows the modulation of the ventral flip measured at each wing beat. The changes between successive wing beats could be as great as 70 μs. Control tests using artificial pulse trains indicated that instability of the digital processing circuitry or the tape recorder motor could not account for this jitter, although it was difficult to rule out completely the contribution of temporal instabilities in the analog peak detector circuits used to trigger the ventral flip events. Nevertheless, it is at least possible that the fluctuations shown in Fig. 2 could represent actual rapid alterations of ventral-flip timing.

The typical relationship between modulation of flip timing and wing-beat amplitude is indicated in Fig. 3A. In most open-loop experiments the two behaviors were strongly correlated: an increase in the wing-beat amplitude of one wing was coordinated with an advance of flip timing of the same wing. In an attempt to uncouple the two behaviors, we examined the responses of six flies to an oscillating vertical stripe at five different frequencies (0.031, 0.1, 0.31, 1.0 and 3.1Hz). The flip timing and amplitude waveforms were then fitted with sine waves by the least-squares method, and the gain and phase were plotted as shown in Fig. 3B,C. When examined in this way, there are no striking differences between the frequency response of flip timing and amplitude modulation, and both behaviors show a decline above 1Hz. McCann (1974) has shown that a similar decay of frequency response in the flight torque of *Calliphora* cannot be explained by temporal limitations of primary photoreceptors or cells within the optic lobes, and presumably arises downstream in descending interneurons or the thoracic motor circuitry. In our study, the phase lag between the behavioral response and stimulus position are scattered around 180°, suggesting that the animal tracks the position and not the velocity of the vertical stripe. This is expected from the well-characterized differences between figure and ground discrimination in flies (Reichardt and Poggio, 1979). The greater scatter of phase values at 3.1Hz is primarily due to the difficulty of estimating phase when the size of the response amplitude is small.

By using torque meters with sufficient temporal resolution, Heisenberg and Wolf (1979, 1984) discovered that, in addition to slower baseline modulation of yaw forces, *Drosophila* generate torque spikes. These transient alterations in torque correspond to rapid body saccades seen in free flight (Bülthoff *et al.* 1980). Although there have been no simultaneous real-time measurements of flight torque and wing kinematics, careful examination of wing motion during optokinetic stimulation reveals rapid alterations in stroke amplitude that are almost certainly the kinematic correlates of torque spikes (Götz *et al.* 1979; Götz, 1983). In the present experiments, these events are most obvious at visual stimulus frequencies of 0.1Hz and below, and they were almost invariably accompanied by transient alterations in ventral-flip timing (Fig. 4). Consequently, rapid changes in ventral-flip timing must also be considered as a possible cause of torque spikes.

Although the modulation of ventral-flip timing and amplitude appear similar when responses are averaged as in Fig. 3, a different picture emerges when scrutinizing details
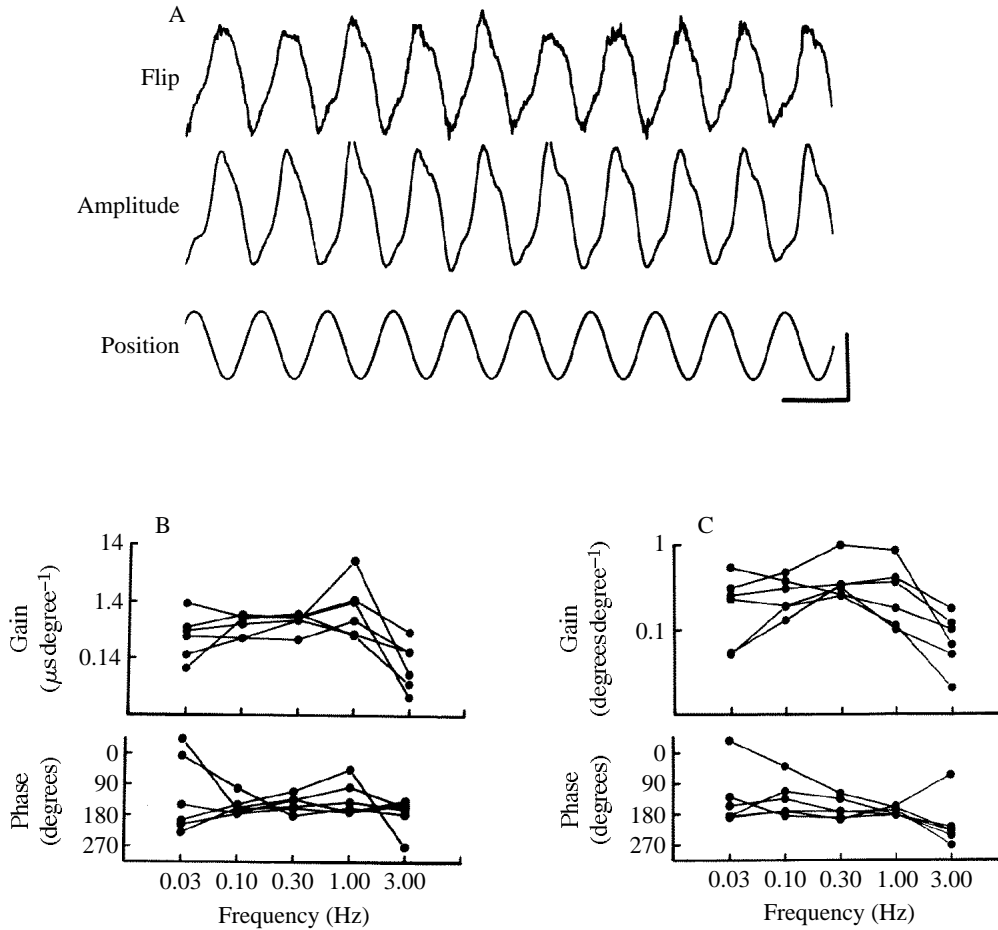
Fig. 3. The modulation of wing-beat amplitude and ventral flip timing is strongly correlated. (A) During 0.5Hz sinusoidal oscillation of the visual stimulus, the modulation of wing-stroke amplitude and ventral-flip timing are correlated such that when the stripe moves to the fly's left, the right wing travels through a greater wing stroke than the left wing and flips in advance of the left wing. (B,C) Records similar to those shown in A at five different frequencies were fitted with sinusoids by the least-squares method to yield an amplitude ratio (gain) and phase between the stimulus (stripe position) and the two behavioral responses (ventral flip timing in B, wing-beat amplitude in C). Data from six individuals are shown. In C, values of gain represent the angular modulation in wing-beat amplitude per degree change in stripe position; those in B represent the change in flip timing per degree change in stripe position. The frequency responses of the two behavioral components are similar. The response phase for both ventral-flip timing and wing-beat amplitude cluster around 180°, indicating that the behaviors track the position of the vertical stripe and not its velocity. Calibration bars: flip timing ±70μs; wing-beat amplitude ±10°; stripe position ±90°; time 0.5s.

of individual flight records. Fig. 5 presents data from flies in which the coordination of flip timing and amplitude is either permanently or temporarily 'decoupled'. Fig. 5A shows a record from a fly in which the flip timing is modulated as usual, but the
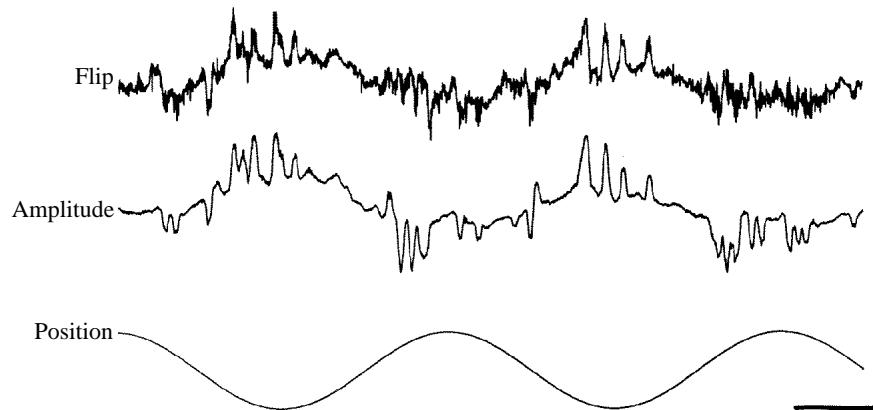
Fig. 4. Both wing-beat amplitude and ventral-flip timing display transient changes reminiscent of torque spikes. The figure displays the response of a fly to 0.1Hz oscillation of a vertical stripe. The transient changes in ventral-flip timing and wing-beat amplitude ride on top of slower baseline modulations that track the stimulus. The transient changes occur primarily during the extremes of pattern position. The sign of the transients is such that when the stripe is to the animal's right, the wing-beat amplitude and flip advance of the left wing are increased relative to the right wing, and *vice versa* when the stripe moves to the animal's left. Calibration bars: flip timing ±70 μs; wing-beat amplitude ±10˚; stripe position ±90˚; time 2.5s.

amplitude modulation is reversed from its typical orientation such that the stroke amplitude is larger on the *inside* of an intended turn and is thus out of phase with ventral-flip modulation. The coordination between the ventral-flip timing and wing-beat amplitude is not rigidly switched, however, as indicated by transient reversals of both behaviors. During one half-cycle (Fig. 5A, circle), the fly rectifies stroke amplitude so that it is transiently in phase with wing-beat amplitude and both behaviors are in their normal orientation. Later in the same record (Fig. 5A, arrows), ventral-flip modulation transiently rectifies during several stimulus cycles as the dark stripe travels through its left-most position. These observations of transient reversals are important for two reasons. First, they indicate that the typically rigid relationship between wing-beat amplitude and flip timing is not merely an artifact resulting from the optical measurement technique. Second, they indicate that the fly has a certain degree of independent control over the two behaviors.

   After long bouts of open-loop stimulation, the flies did not usually respond vigorously to the visual stimulus. During such instances, the decoupling of amplitude and flip were quite common. In the record shown in Fig. 5B, the fly responded to approximately every third oscillation cycle and, in nearly every case, the wing-beat amplitude and flip modulation are out of phase. As was typical in such events, it was the amplitude modulation that was reversed from its normal orientation.

   One possible explanation for the breakdown of normal coupling between wing-beat amplitude and flip timing is that certain individuals were either behaviorally aberrant or improperly mounted to the tungsten rod with the adhesive. It was possible to discount this
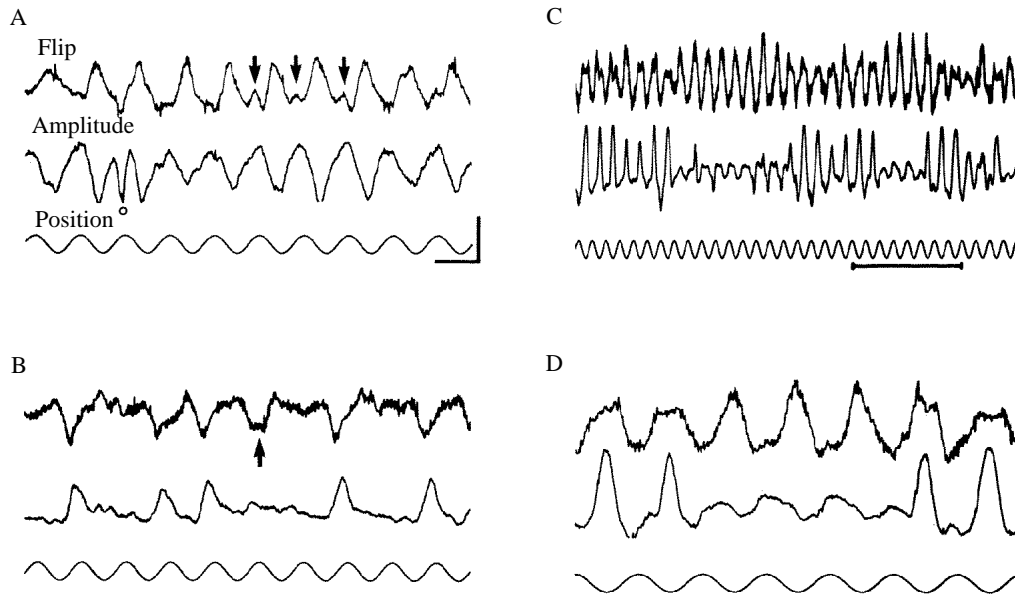
Fig. 5. The modulations of ventral-flip timing and wing-beat amplitude are not rigidly coupled. The figure displays several examples in which the normal correlation between flip delay and stroke amplitude is reversed or disrupted during open-loop stimulation at 0.5Hz. (A) In this example, the modulation of wing-beat amplitude is opposite from its typical orientation. Thus, the wing on the outside of the fictive turn flips in advance, but has a smaller wing stroke. Note, however, transient rectifications of flip timing (arrows) and wing-stroke amplitude (circle), which momentarily bring the two behaviors into register. (B) In this example, the fly fails to respond to approximately every other oscillation cycle and, in each case, the wing-beat amplitude modulation is reversed from its typical orientation. Also note a transient modulation of ventral-flip timing with only a small change in wing-beat amplitude (arrow). (C) This example shows the flight record of a fly that spontaneously changes the coupling between wing-beat amplitude and ventral-flip timing. (D) Expansion of the segment indicated by the bar in C. At the beginning and end of the record the modulation of flip timing and stroke amplitude display their normal orientation. For three stimulus cycles in the middle, however, the coupling between the two behaviors is reversed. Note that, during the portion in which the magnitude of wing-beat amplitude modulation decreases, there was a slight increase in the magnitude of flip timing modulation. Calibration bars: flip timing $\pm70\,\mu$s; wing-beat amplitude $\pm10°$; stripe position $\pm90°$; time 2s in A, B; 6s in C; 0.6s in D.

hypothesis, however, in repeated experiments on the same individual. Moreover, in some instances, flies appeared spontaneously to switch back and forth between discrete flight modes with qualitatively different forms of coordination between wing-beat amplitude and ventral-flip timing. Fig. 5C,D shows such an example in which periods of normal amplitude-flip modulation are interspersed with periods lasting several seconds during which the fly qualitatively altered the pattern of coordination. The expanded trace in Fig. 5D illustrates the complexity of this coordination. The wing-beat amplitude trace appears to consist of the sum of two sinusoidal wave-forms: a low-magnitude response that is about 200° out of phase with flip timing, and a larger response that is in phase with
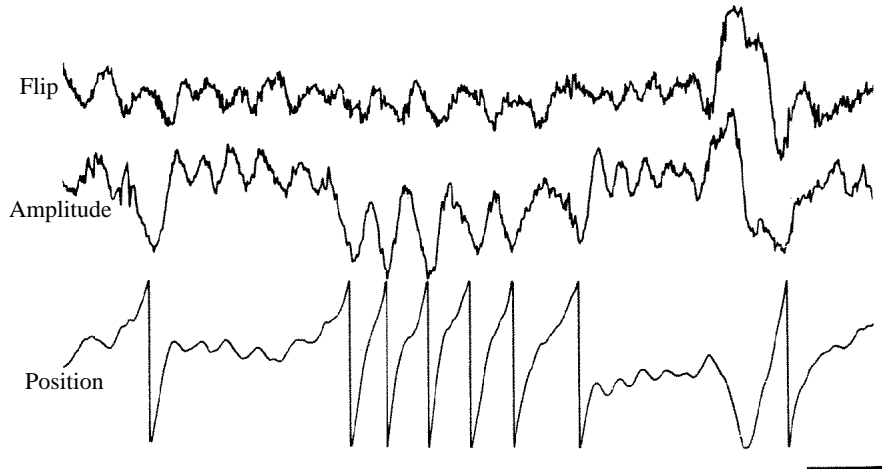
Flip

Amplitude

Position

Fig. 6. The normal correlation between stroke amplitude and ventral-flip timing modulation may be disrupted in the closed-loop condition. The record was taken from a closed-loop experiment in which the fly's own behavior controlled the position of the visual stimulus. In this example, the control signal consisted of a linear difference between the flip-timing signal and the amplitude difference (flip timing minus amplitude). Thus, phase advance of the left wing would correctly move the visual stimulus to the right, whereas an increase in stroke amplitude of the left wing would inappropriately move the stimulus to the left. The weights of the two control signals were arbitrarily adjusted in order to stabilize the flight conditions. The fly responded to this closed-loop arrangement with long flight segments in which flip phase and stroke amplitude were reversed from their typical orientation. The inverse correlation is not rigid, as indicated by instances in which the two behaviors display normal coordination. Calibration bars: flip timing ±70 μs; wing-beat amplitude ±10°; stripe position ±90°; time 2.5s.

flip modulation. The fly was able to turn off this latter response for several stimulus cycles without affecting the former.

The ability of flies to control wing-beat amplitude and ventral-flip timing independently was also seen during closed-loop experiments in which the velocity of the visual stripe was controlled by the animal's own behavior (Heisenberg and Wolf, 1984; Götz, 1987*a,b*). Fig. 6 shows a short segment of such a closed-loop experiment in which the control signal consisted of a linear difference between the flip timing signal and the wing-beat amplitude signal. Thus, in order to stabilize the velocity of the stimulus stripe, the fly must modulate flip timing appropriately and modulate amplitude signal with reversed orientation. In this example, the protocol had the desired effect of disrupting the typical correlation between the two behaviors. As in the open-loop condition, however, the coupling between wing-beat amplitude and flip modulation is not rigid, as indicated by the instance in which the two behaviors are transiently in phase near the end of the trace (Fig. 6). As with the open-loop experiments, this result indicates that the flies can exert some degree of independent control over flip timing and stroke amplitude.

Discussion

This paper introduces a previously unknown component to the turning response of *Drosophila:* modulation of ventral-flip timing. During tethered flight experiments, this behavior is typically well coordinated with changes in wing-beat amplitude. However, as indicated by both closed-loop and open-loop experiments (Figs 5, 6), the coupling is not rigid, and flies are capable of exerting at least some independent control over the two behaviors. These results raise issues at both the aerodynamic and neurobiological levels. First, how does direct flight musculature responsible for steering movements independently control flip timing and wing-beat amplitude? Second, how might these two behaviors interact in the production of aerodynamic forces?

Neuromuscular control

In flies, the control of steering movements resides in a set of 17 small tubular muscles that insert directly within the region of the wing hinge (Pringle, 1957; Heide, 1971*a*,*b*). Unlike the large stretch-activated fibrillar power muscles that generate the gross movements of the wings, the steering muscles are synchronous and are thus capable of fine-tuned control from the central nervous system. The activity of only five of the 17 non-fibrillar muscles has been examined during tethered flight (Heide, 1971*a*,*b*, 1975, 1983; Spüler and Heide, 1978; Götz, 1983; Egelhaaf, 1989; G. Heide and K. G. Götz, in preparation). The firing rate of four muscles (M.III1, M.I1, M.b2 and M.hg3; using the nomenclature of Heide, 1971*a*) appears to be correlated with changes in wing-beat amplitude elicited by optokinetic stimuli in *Drosophila, Calliphora* and *Musca*. Although these muscles appear to act tonically, they tend to fire in phase bands synchronized with the wing stroke (Heide, 1975, 1983). One of the three muscles that inserts on the basalar process, M.b2, does effect an advance in the timing of the ventral flip of the ipsilateral wing when artificially stimulated during tethered flight (Lehmann and Götz, 1992). However, stimulation of M.b2 also causes a *delay* in the translation of the same wing during the clap-and-peel motion of the dorsal reversal. This effect with electrical stimulation of M.b2 is opposite to that occurring normally during optokinetic stimulation, in which an advance in flip timing is accompanied by an advance in translation during the clap-and-peel one half-stroke later. This discrepancy, together with the fact that flies possess at least a limited ability to modulate wing-beat amplitude and rapid supination independently, argues that more muscles must be involved in the temporal control of the ventral flip.

One muscle that seems to be particularly well suited as a candidate for control of the ventral flip is M.b1 (pa4 in the nomenclature of Zalokar, 1947; B2 of Ewing, 1979), which also inserts on the basalar process. In contrast to all the other direct muscles examined, M.b1 is unique in that it typically fires an action potential during every wing beat in all three Dipteran genera examined so far (*Drosophila*: Ewing, 1979; Götz, 1983; Heide, 1983; *Calliphora*: Heide 1971*a*, 1975, 1983; *Musca*: Heide, 1975; Egelhaaf, 1989), whereas the other direct flight muscles are typically active only during turning maneuvers. Consequently, M.b1 is the one muscle that would be capable of controlling ventral-flip timing on a wing-beat by wing-beat basis. The narrow phase band of M.b1 activity within

the wing-stroke cycle is tuned entirely by wing-beat synchronous afferents on the wings and halteres (Heide, 1983; Miyan and Ewing, 1984). The activity of M.b1 is not without variability: the firing rate of the muscle on the side towards the inside of visually induced turns tends to drop in *Musca* (Heide, 1975; Egelhaaf, 1989) and, in *Drosophila* and *Calliphora*, it skips occasional wing beats (Heide, 1983). Still, the ability of this synchronous muscle to fire at wing-beat frequency for extended periods is quite remarkable. If the M.b1 homolog in gnats, mosquitoes and other small dipterans has similar characteristics it could be among the fastest known synchronous muscles in any animal. In accordance with these rates, it is not surprising that the diameter of the M.b1 motor neuron axon may exceed 15 μm in both *Drosophila* (King and Tanouye, 1983) and *Calliphora* (Heide, 1983). This diameter is comparable to that of the giant fibers of the escape reflex pathway (King and Wyman, 1980). King and Tanouye (1983) found no other comparably sized motor axons in their extensive analysis of the *Drosophila* flight system.

It is not simply the possession of a rapid firing rate that most strongly implicates M.b1 in the control of the ventral flip; indeed, other steering muscles may be capable of firing at wing-beat frequency (Heide, 1975). However, M.b1 displays changes in firing phase elicited by visual stimuli that are qualitatively similar to the modulation of ventral-flip timing under similar conditions. In the presence of optokinetic stimulation, the muscle on the outside of an induced turn fires in advance of its contralateral partner (Heide, 1983; Götz, 1983; Egelhaaf, 1989; G. Heide and K. G. Götz, in preparation). The absolute changes in phase are quite different between the two phenomena: visual stimuli can elicit a phase difference of 60° between the left and right M.b1 spikes, whereas changes in ventral-flip timing rarely exceed 10°. However, such a quantitative discrepancy is not necessarily inconsistent with a role for M.b1 in the ventral flip. Large changes in the activation phase of one muscle are likely to produce only small changes in the timing of wing rotation, since the latter is also influenced by the activity of many other direct and indirect flight muscles through the complex mechanics of the wing hinge.

Could M.b1 actually modulate motor activity at wing-beat frequency? Isometric force measurements of M.b1 in *Calliphora* indicate that the muscle approaches a fused tetanus when stimulated at wing-beat frequency (Bergmann-Erb and Heide, 1990), which suggests that it would be incapable of modulating wing motion on a wing-beat by wing-beat basis. However, this isometric performance may be misleading, since during flight, M.b1 must undergo a cyclical length oscillation during each wing beat as the basalar sclerite is moved back and forth. As has been demonstrated for the synchronous flight muscles of orthopteran insects (Josephson, 1985*a,b*), the total power output of an oscillating muscle will depend upon the amplitude of the imposed oscillation as well as upon the timing of electrical excitation within each loading cycle. Both the dynamic stiffness and work output of M.b1 are indeed strongly dependent on the phase of electrical activation when the muscle is oscillated mechanically at wing-beat frequency (Tu and Dickinson, 1992). Thus, changes in activation phase during flight could allow for wing-beat by wing-beat modulation of active mechanical properties.

Correlation between wing-beat amplitude and ventral-flip timing

Studies of tethered *Drosophila* reveal a relatively simple speed and altitude control

system in which the fly generates an aerodynamic force vector of constant orientation with respect to its stroke plane. By analogy with a helicopter, changes in flight forces are controlled by alterations of the stroke plane which, in turn, are accomplished by rotations of the entire body axis (Vogel, 1966; Götz, 1968; David, 1978, 1985; Götz and Wandel, 1984; Zanker, 1988b). However, more recent studies suggest that the flight control system may be more complex than this simple helicopter model would imply. Studies of free flight in *Musca* and *Drosophila* indicate that these flies have the ability to change the orientation of the net aerodynamic force vector without tilting the stroke plane (Wagner, 1986; Ennos, 1989). Furthermore, the actuator disc model does not seem to be adequate to explain the changes in force orientation required for yaw responses. The yaw control system of *Drosophila* involves a large suite of behaviors, including changes in stroke amplitude, abdominal flexion and leg bending (Vogel, 1967; Götz, 1968, Götz *et al.* 1979; Zanker, 1990b). Early studies of force production in flies identified a slow linear torque produced in response to a yaw stimulus (Götz, 1964, 1968; Blondeau and Heisenberg, 1982). However, by measuring flight torque with high temporal resolution, Heisenberg and Wolf (1979, 1984) have argued that much course control in *Drosophila* involves rapid *torque spikes,* which are generated over a few wing beats and correspond to the body saccades displayed in free flight (Land, 1973; Land and Collet, 1974; Bülthoff *et al.* 1980). Changes in wing-beat amplitude are thought to be primarily responsible for both the slow linear changes in torque and the generation of torque spikes (Nachtigall and Roth, 1983; Götz *et al.* 1979; Götz, 1983; Heisenberg and Wolf, 1984; G. Heide and K. G. Götz, in preparation). However, the application of quasi-steady-state theory to measured wing-beat amplitude differences yields yaw forces that are an order of magnitude smaller than those actually produced by the fly (Zanker, 1990b). Therefore, it is likely that other behaviors besides wing-stroke modulation are important in yaw control, and that the actual forces are generated by unsteady mechanisms.

The best-characterized unsteady mechanism in *Drosophila* is the *clap-and-fling,* or *clap-and-peel*, behavior which occurs during the upstroke to downstroke transition. (Weis-Fogh, 1973; Lighthill, 1973; Ellington, 1980, 1984b; Götz, 1987a). Zanker (1990b) has suggested that bilateral asymmetries in the clap-and-peel might be used by the fly to generate yaw torque, but also reports that the use of the clap-and-peel diminishes with increasing air speed in tethered flight experiments. Similarly, Ennos (1989) found little evidence of clap-and-fling in an analysis of free-flying *Drosophila*. Thus, it is unlikely that bilateral changes in the kinematics of clap-and-peel could be entirely responsible for the generation of yaw forces in *Drosophila*. This must be the case for larger flies such as *Musca* and *Calliphora* that do not display clap-and-peel behavior. One alternative unsteady mechanism for cruise control is the production of yaw forces by alteration of ventral-flip timing between the two wings.

How might the ventral flip affect the production of flight forces? Nachtigall (1979) first suggested that the wing rotation during stroke reversal might function to increase circulation during the subsequent upstroke. Ellington (1984b) has discussed more extensively the mechanisms by which isolated wing rotation might affect the shedding of the bound circulation from the downstroke and the generation of the opposite-sense circulation required for the subsequent upstroke. Although the morphological axis of

rotation of insect wings typically resides near the one-quarter chord line, he argued that wing flexion could act to keep the trailing edge stationary during supination and to allow the leading edge to swing, where the large shear forces would then favor the development of a separation bubble. Although *Drosophila melanogaster* wings do not flex during supination (Zanker, 1990*a*), rotation about the trailing edge could still be achieved by delaying the timing of supination relative to stroke reversal (Ellington, 1984*b*; Ennos, 1989). A recent study of force production by *Drosophila* wing models accelerated from rest (Dickinson and Götz, 1993) suggests that the wings are capable of generating transient forces at the start of translation due to a large attached vortex that is present at high angles of attack. The magnitude of these forces on model wings can be greatly augmented if translation is preceded by rotation (M. H. Dickinson, in preparation), as suggested by Ellington's flex model. Evidence that large forces are indeed generated during ventral stroke reversal comes from instantaneous measures of flight forces in tethered *Drosophila* indicating a sharp force peak near the time of the ventral flip, which exceeds that produced during the downstroke (Zanker and Götz, 1990).

Assuming that the ventral flip does function to enhance a large transient force during the early stages of the upstroke, how might these forces be used by the fly for active course control? Flies could potentially control yaw forces in one of three ways: through inter-wing differences in the timing, the magnitude or the spatial orientation of the ventral-flip transients.

Even if the forces generated by the two wings were equal in magnitude and of symmetrical orientation, time delay alone might be sufficient to generate a net torque. However, this hypothesis requires that torque produced during the ventral flip should generate significant angular acceleration of the body. Owing to the viscous drag on the body at the Reynolds number range appropriate for fly flight, this acceleration is likely to be quite small (Reichardt, 1973; Heisenberg and Wolf, 1984). It is improbable, therefore, that timing differences in the ventral flip could alone be responsible for modulation of yaw torque in *Drosophila*.

Changes in the magnitude of force production by the two wings is the most obvious route to yaw torque, and could be controlled by modulating the size of the leading-edge separation bubble generated at the start of the upstroke. One likely source of such modulation for the fly is through temporal control of wing translation and rotation during the downstroke-to-upstroke transition. For the following discussion, it is important to distinguish between the two critical elements of the downstroke-to-upstroke transition: the ventral flip (the rapid change in wing angle of attack) and stroke reversal (the rapid change in the direction of wing translation). Unfortunately, although current methods allow measurement of ventral-flip timing, they do not accurately resolve changes in the timing of stroke reversal. As argued above, the timing between these two events is important because it affects the functional axis of wing rotation and, consequently, the amount of shear at the leading edge. Assuming that stroke reversal is synchronous on the two wings, an advance of the flip on one wing should produce less shear about the leading edge and, consequently, a smaller unsteady force transient on the upstroke. But since the wing on the outside of a turn rotates in advance, this would lead to a flight torque away from the turning stimulus, contrary to what is measured in yaw-torque flight arenas under

similar conditions (Götz, 1968; Heisenberg and Wolf, 1984). However, it is probably not safe to assume that stroke reversal is synchronous on the two wings during turning maneuvers. In *Drosophila,* most of the changes in stroke excursion during turning maneuvers affect the ventral portion of the wing stroke. This extension of the ventral portion of the wing-beat envelope is accomplished by an increase in translation velocity during the downstroke (Zanker, 1990*b*). The absence of a corresponding increase in upstroke velocity suggests that there must be a net *advance* in the timing of stroke reversal, since only an increase in the wing velocity during both strokes could result in synchronous stroke reversal with asymmetrical stroke amplitude. Thus, although the ventral flip is advanced on the outside of the turn, it could be either delayed or advanced relative to stroke reversal depending upon the temporal shift accompanied by an increase in wing-beat amplitude. Unfortunately, the exact sign of the relative timing between the ventral flip and stroke reversal cannot be ascertained without more precise temporal and spatial resolution of the wing kinematics during turning maneuvers. This has proved to be a difficult task when using a small fly that beats its wings 200 times each second. These difficulties aside, it is possible that the enlargement of wing-beat amplitude is important not because it reflects an increase in stroke length *per se*, but rather because it affects the relative timing between stroke reversal and wing supination and, thus, the production of unsteady forces at the initiation of the upstroke. This model suggests a quite different role for wing-beat amplitude from that proposed by the classical quasi-steady-state view.

The magnitude of aerodynamic transients produced at the onset of the upstroke will also almost certainly depend upon the speed of supination, as well as its timing relative to stroke reversal. Careful examination of the shadow signals generated in our apparatus indicates that an advance in ventral-flip timing is usually accompanied by an increase in rotation velocity. Such changes in rotation velocity should have a strong effect on shear rates and the resultant formation of a leading-edge bubble.

Finally, even if the relative timing between the ventral flip and stroke reversal remained constant, the fly might generate yaw torque quite simply through differences in the position of the two wings during the downstroke-to-upstroke transition and, thus, in the orientation of the resultant forces. This is an appealing general hypothesis, because appropriate coordination of wing position at the time of the ventral flip could generate forces for the control of yaw, pitch and roll. Once again, such a scheme predicts a rather different role for wing-beat amplitude from that proposed by classic quasi-steady-state theory: stroke amplitude is important because it reflects the geometric position of the wing at the time of the ventral flip.

In summary, the recognition that flies actively regulate the timing of wing rotations, together with a growing understanding of unsteady aerodynamic mechanisms, suggests new mechanisms that might be relevant for the flight control of *Drosophila* and other insects. The control of the ventral-flip force transients would offer a rapid and flexible system of steering that could explain how flies alter the direction of yaw and other flight forces without changing the angle between the stroke plane and the body axis (Wagner, 1986; Ennos, 1989). According to this hypothesis, the fly is capable of precise flight control by modulating the relative timing of wing rotation and stroke reversal, the absolute speed of those rotations and the geometric position of the wings when the

rotations occur. In addition, changes in wing-beat amplitude are seen as playing a quite different role through their effect on the timing and spatial orientation of the wings at stroke reversal. Although the model is conjectural at this point, it should be quite possible to test its predictions by measuring wing-beat amplitude and ventral-flip timing while simultaneously monitoring instantaneous flight torque.

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